

The Ordovician Graptolites of Spitsbergen



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Synopsis

The Valhallfonna Formation, northern Ny Friesland, Spitsbergen, includes 56 species and subspecies of graptoloids, which occur in intimate association with rich trilobite faunas. The faunas range in age from early Arenig (Bendigonian) to probably earliest Llanvirn. The Arenig age faunas of the Olenidsletta Member include a number of samples of beautifully preserved, isolated material, from horizons which have never hitherto yielded such well-preserved specimens. These contribute to an understanding of general phylogenetic relationships in the early history of dichograptoids.

We introduce some revisions in the descriptive terminology and thecal notation system for dichograptoid graptoloids. The principles of classification of these graptoloids are discussed, and a system based on early rhabdosome development is preferred. It is established that the isograptid development type (with $th1^2$ dicalyal) is primitive for the Graptoloidea, and it is the rule for our Arenig species. The *artus* development type (formerly, and incorrectly, termed the *bifidus* type), with $th1^1$ dicalyal, is secondarily derived from the isograptid type. Two major development styles are recognized in graptoloids with dichograptid grade of organization: these characterize the families Dichograptidae and Phyllograptidae, both redefined here.

Three subfamilies are recognized in the Dichograptidae: Dichograptinae, Isograptinae and Sigmagraptinae nov., the last defined by a slender proximal end with a characteristic structure. In general we employ the well-established form-genera (*Didymograptus*, *Tetragraptus*), using subgenera to typify phylogenetic groupings within genera; one new such subgenus, *Didymograptus* (*Didymograptellus*) is proposed. The development and fine structure of the type species of *Phyllograptus*, *P. typus*, shows that it is not related to superficially similar phyllograptoids of the *angustifolius* group: for these the new dichograptid genus *Pseudophyllograptus* (type species *P. angustifolius* Hall) is proposed. *Phyllograptus* in the restricted sense is related to a group of extensiform 'didymograptids' which are placed in the new genus *Xiphograptus* (type species *D. formosus* Bulman). *Xiphograptus* and *Phyllograptus* together constitute the Phyllograptidae.

In addition to the foregoing, the following new taxa are proposed: *Laxograptus* gen. nov. (a sigmagraptine, type species *Zygograptus irregularis* Harris & Thomas); *Dichograptus maccoyi densus* subsp. nov.; *Tetragraptus contrarius* sp. nov.; *Tetragraptus phyllograptoides triumphans* subsp. nov.; *Didymograptus* (*Didymograptellus*) *multiplex* sp. nov.; *Pseudophyllograptus angustifolius* chors subsp. nov.; *Isograptus scandens* sp. nov. *Pseudotrigranograptus* exists in both triserial and quadriserial morphs; for the former the specific name *P. minor* Mu & Lee is employed, for the latter *P. ensiformis* (Hall).

Lectotypes are designated for the following species of J. Hall (1858, 1865): *Tetragraptus bryonoides*, *Didymograptus extensus*, *D. similis*, *D. patulus*, *Phyllograptus typus*, *P. ilicifolius*, *P. angustifolius* and *P. anna*; also for *Tetragraptus amii* and *T. reclinatus* Elles & Wood 1902, and for *Tetragraptus serra* (Brongniart 1828) the type specimens of which have been rediscovered.

The Spitsbergen graptolites are typical of the Pacific Province, and the Australian and New Zealand succession can be matched zone by zone in the Valhallfonna Formation. Stratigraphic distribution of the species shows that the Arenig Series divides naturally into three; Lower Arenig, *approximatus* faunas at base and extending upwards to the diverse later Bendigonian; Middle Arenig, an interval characterized by the first radiation of pendent didymograptids and true *Phyllograptus*; and Upper Arenig, the major radiation of the isograptids, with *Pseudotrigranograptus* and *Xiphograptus*. *Pseudophyllograptus* occurs in the Lower and Upper, but not the Middle Arenig in Spitsbergen. This tripartite division is probably generally applicable in the Pacific Province. Equivalents of what we here term Upper Arenig are attenuated or absent on platform sequences on what were separate continental blocks in the early

Ordovician; this is probably attributable to the effects of a major marine regression coinciding with Upper Arenig (= Valhallan Stage) deposition in Spitsbergen.

Introduction and acknowledgements

This paper describes the Ordovician graptolites from the Valhallfonna Formation (Arenig–?Llanvirn), Ny Friesland, northern Spitsbergen. The graptolite fauna in the Valhallfonna Formation is a varied one. Although much of the material is preserved as flattened rhabdosomes, a number of species are preserved in relief, and can be isolated from the rock by solution in acid. Very few graptolites of this age have been described from isolated material, and it is our belief that this new information contributes to an understanding of the phylogeny of the Graptoloidea as a whole. From a stratigraphical point of view the Valhallfonna graptolites are of special importance because they occur with possibly the richest trilobite faunas of any succession of early Ordovician age, which have been described in a series of papers by Fortey (1974, 1975*a*, 1980*a*). There is no other section on the North American Ordovician plate where such a rich Arenig graptolite assemblage can be directly linked with a succession of trilobite faunas. The Valhallfonna sequence is also a thick one, and there is every reason to suppose that the succession of graptolite faunas recorded in it is complete; bed-by-bed collecting has enabled refinements to be made to the zonal sequence of graptolite faunas.

The material which forms the basis of this paper was collected either by the Cambridge University Expedition of 1967, or by that run by the Norsk Polarinstitut and the Paleontological Museum, Oslo in 1972. Specimens are stored in the Sedgwick Museum, Cambridge (SM), the Paleontological Museum, Oslo (PMO) and British Museum (Natural History). Many of the species names employed here have a long history, and in many cases we have examined type material to support our determinations. The following have assisted us in the search for specimens in their collections: Dr T. E. Bolton, Geological Survey of Canada, Ottawa; Dr J. N. Krumdieck, New York State Museum; Miss E. Lilljehall, Geological Collections, Lunds Universitet, Sweden; Dr R. B. Rickards, Sedgwick Museum, Cambridge; Dr A. W. A. Rushton, Institute of Geological Sciences, London; Dr D. L. Bruton, Palaeontological Museum, Oslo. The larger part of the contribution of R.A.C. was completed during the tenure of a Nuffield Travelling Fellowship and a Study Award supported by the Department of Scientific and Industrial Research, New Zealand, which are gratefully acknowledged. Most of the photography was undertaken by the Photographic Unit of the British Museum (Natural History).

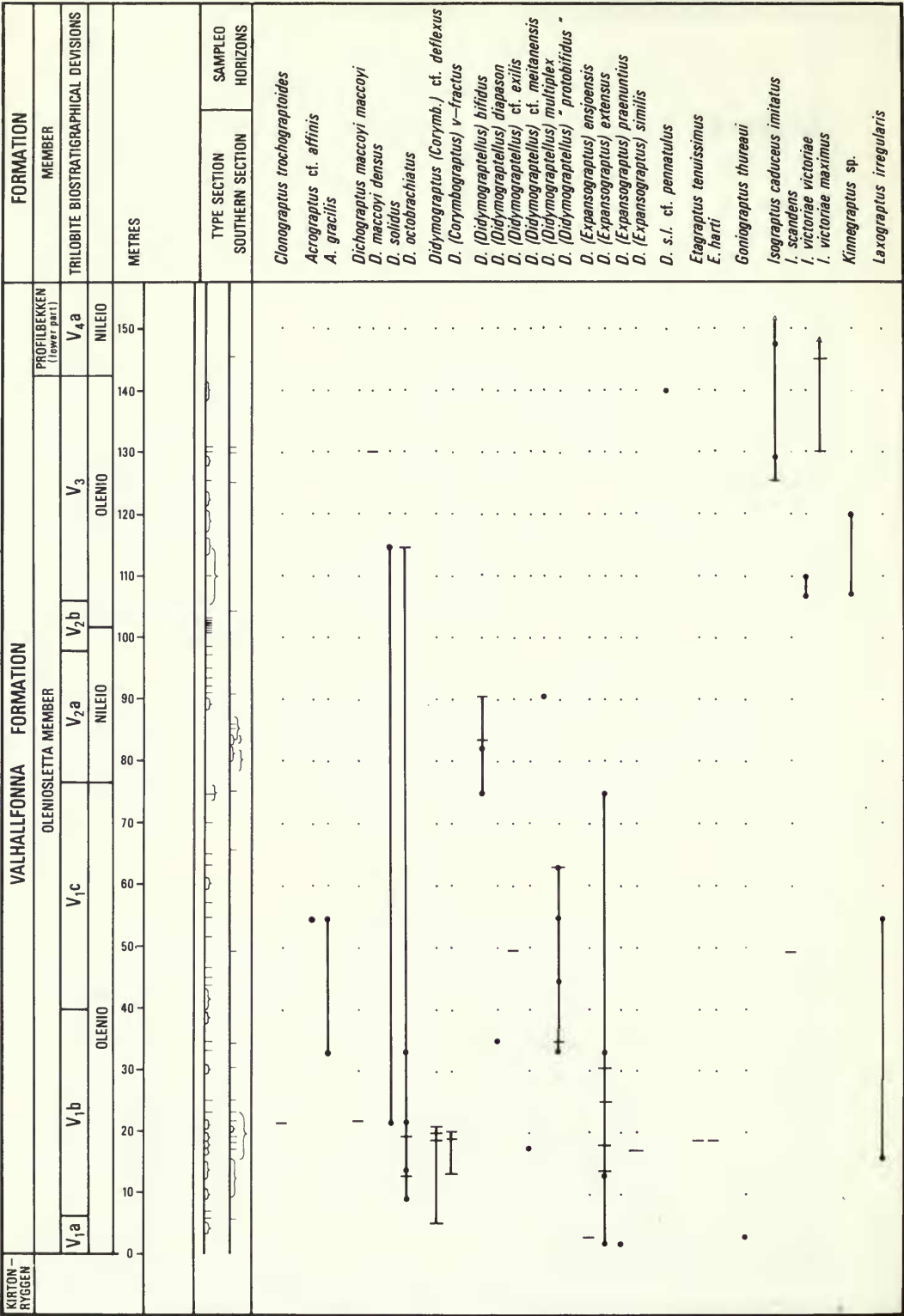
Stratigraphy

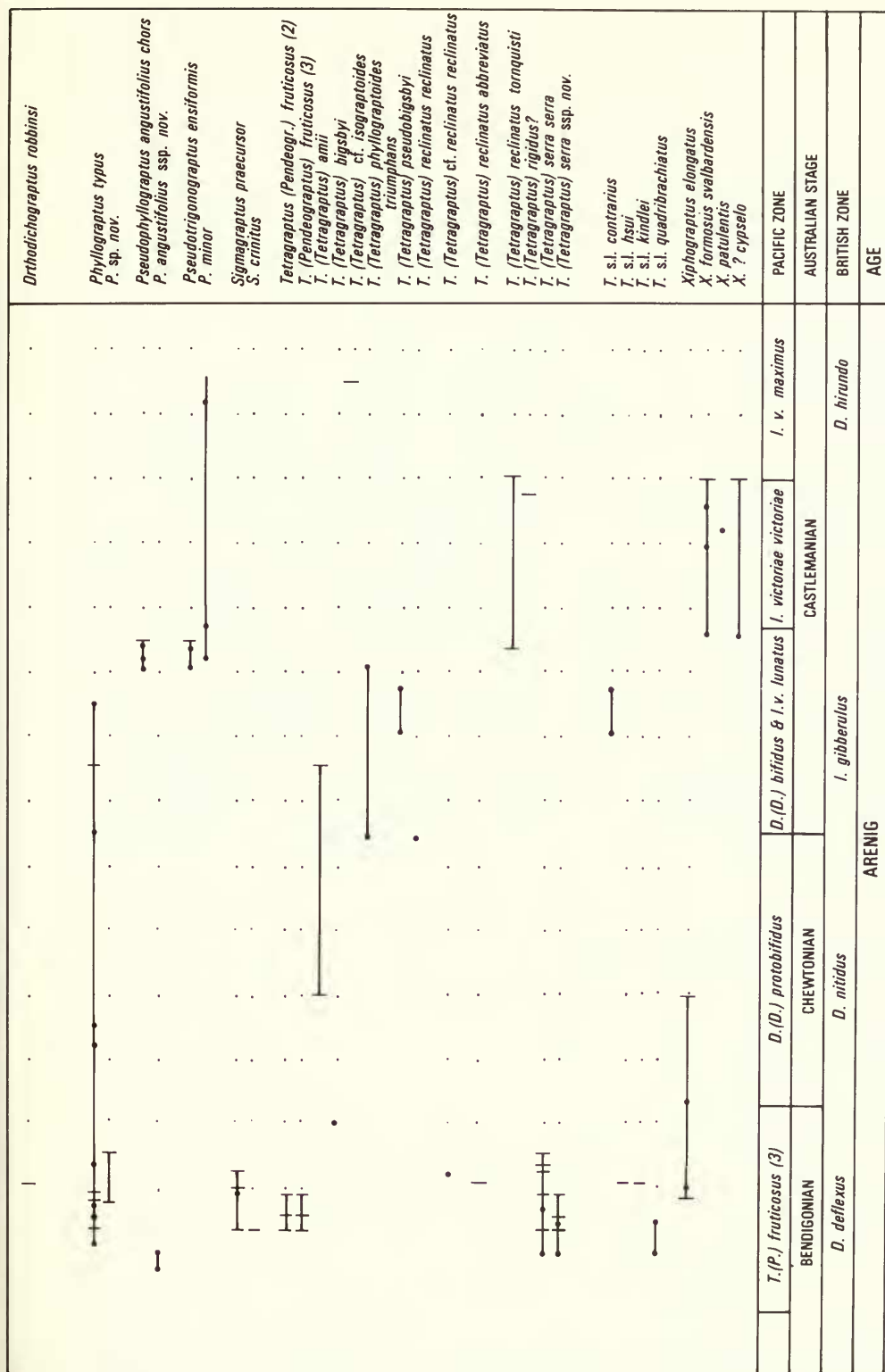
The regional geology, general stratigraphy and lithologies of the Valhallfonna Formation were described by Fortey & Bruton (1973) and Fortey (1975*b*). Specific comments on the age of the graptolite faunas have been given by Fortey (1971, 1976, 1980*a*) and Archer & Fortey (1974). Our more detailed work on the graptolites confirms in general the age determinations of the earlier work, although we now have a more refined biostratigraphy. The Valhallfonna Formation was deposited over a period extending from the early Arenig (Upper Bendigonian = higher part of the *T. fruticosus* Zone) to probably the earliest Llanvirn. The most prolific faunas are found in the lower unit, the Olenidsletta Member, which is generally developed in deeper water facies than the overlying Profilbekken Member. The Olenidsletta Member includes the Bendigonian faunas at its base and extends into the high Castlemainian. A more detailed account of the sequence of faunas is given below.

Occurrence of the graptolites

Graptolites occur in three main types of preservation in the Valhallfonna Formation:

1. As flattened impressions on dark limestones, lime-shales, or, rarely, fine silty shales without carbonate. This last is the 'usual' mode of preservation of graptoloids. Fine details of





thecal structure are obscured. Generally the periderm is black and carbonized and hence hard to photograph, except in the rare cases where they have acquired a silvery sheen. We have to rely on line drawings to illustrate this kind of material.

2. In relief in limestone, but without the capacity for isolation. The periderm in these cases is reduced to a carbonaceous film, which breaks up into unidentifiable black specks on solution in acid. We have used serially ground sections to study fine anatomy of this kind of material, which gives good results. Such preservation is commonest in rather pure limestones, such as those at the top of V₂ in the Olenidsletta Member, and it is possible to infer a good deal about three-dimensional structure even without serial sections (e.g. *Pseudotrigonograptus ensiformis*, p. 249).

3. In relief in limestone, and with periderm well enough preserved for isolation. The commonest lithology for this kind of preservation is an impure, dark limestone with a high silt (and often silica) content. The material described by Fortey (1971) and Archer & Fortey (1974) was from beds of this kind. We now have a spread of such horizons through most of the Olenidsletta Member. In rare cases the material is flattened, although it can still be isolated. Proximal ends are often partially translucent, and growth stages are common enough to reconstruct astogeny. Curiously, most of the productive horizons are almost monospecific. The most striking case of this is perhaps the horizon that yielded the triserial *Pseudotrigonograptus minor* described by Fortey (1971). This species is generally rare in the upper 40 m of the Olenidsletta Member. The bed in which the material which it is possible to isolate occurs is crowded with rhabdosomes at all stages of growth. One must presume that the species lived together in large clots or drifting swarms which, rarely, were overcome *in toto* (plankton bloom?), and, losing buoyancy, ultimately came to rest as a thick layer on the sediment surface. A few specimens of *Xiphograptus formosus svalbardensis* were entrapped at the same time. Another horizon, only a few metres above that with *Pseudotrigonograptus*, is crowded with the rhabdosomes of *X. formosus svalbardensis*, but with *Pseudotrigonograptus* extremely rare, and tetragraptids likewise. There is nothing to suggest protracted non-deposition at such horizons, indeed, it would be difficult to explain the preservation in relief if the specimens were not enclosed by sediment relatively quickly. Some graptoloids may have been gregarious, like some of the open ocean siphonophores today, and monospecific horizons may be the record of foundered swarms of gregarious species. The restricted diversity of these horizons means that in such cases it is relatively easy to associate growth stages with the appropriate mature rhabdosome; the relief specimens command a large share of the present systematic treatment. Many of our species, however, have not been recovered from such horizons, and are known only from flattened examples.

Sequence and correlation of graptolite faunas

The general sequence of graptolite faunas in the Valhallfonna Formation was given by Fortey (1976, 1980b). We have now been able to plot the detailed stratigraphic ranges of the species (Fig. 1), both from the southern and northern sections of the Olenidsletta Member. There is no significant difference in the sequence of faunas between the sections, although some of the best fossiliferous horizons, such as those described in the previous paragraph, are not traceable from one section to the other. For example, one important bed at 50 m from the base of the Olenidsletta Member has yielded a rich fauna in the southern section, including *Isograptus scandens* sp. nov., but has not been found in the northern section.

There is no evidence in the Olenidsletta Member of the earliest Arenig faunas of the *Tetragraptus approximatus* Zone. Strata equivalent to this zone are probably present in the upper part of the underlying Kirtonryggen Formation, which has a fauna very similar to that of the Catoche Formation, western Newfoundland, of probable *T. approximatus* Zone age. Stratigraphic plots of the ranges of the graptoloid species from the Olenidsletta Member show that there is a great deal of overlap between ranges, and hardly any sharp breaks in the sequence, which is no doubt a reflection of the thickness of the succession and a lack of major hiatuses in deposition. Nonetheless it is possible to recognize a succession of zonal assemblages exactly comparable to those recognized in other successions of the Pacific province, such as in

Texas, Australia and New Zealand. In our account we generally refer to the stage names used in the sequence of Victoria, Australia (Thomas 1960), because they include the most refined divisions, but which also have their equivalents in the scheme of Berry (1960), widely used in North America. Correlation with the standard sequence of Great Britain and that of Scandinavia is inferred from more slender evidence (Fig. 2).

TREMADOC		A R E N I G						LLANVIRN		S E R I E S	
<i>Clonograptus</i> 2	approx- atus 3	<i>fruticosus</i> 4 & 5	<i>protobifidus</i> 6	<i>bifidus</i> 7	<i>Isograptus</i> 8	<i>tentaculatus</i> 9		North graptolite	America Zones ¹		
Lancefieldian La 2-3	Bendigonian Be 1-4		Chewtonian Ch 1-2	Castlemanian Ca 1	Yapeenian Ya 1-2	Darriwilian		Australian graptolite sequence ²			
gap		<i>deflexus</i>		<i>nitidus</i>	' <i>gibberulus</i> '	<i>hirundo</i>	' <i>bifidus</i> '	British graptolite zones ³			
gap		<i>C.v-similis</i>	<i>S. tardi- brachiatus</i>	<i>T. raclinatus abbreviatus</i>	? gap	<i>D. retroflexus</i>		Bohemia ⁴			
no graptolites	<i>approximatus</i> & <i>phyllograptoides</i>	<i>validus</i> <i>balticus</i>	<i>densus</i>	<i>elongatus</i>	3b E of Spjeldknaes	? gap	<i>U. Didymogr. shale</i>	Norway ⁵	Scandinavia		
no graptolites	<i>phyllograptoides</i>	<i>balticus</i>	<i>densus</i> + <i>gracilis</i>	<i>densus</i> + <i>elongatus</i>	<i>patulensis</i>	' <i>gibberulus</i> '		Sweden ⁶			
<i>A. sinensis</i>	<i>T. approx- imatus</i>	<i>D. filiformis</i>	<i>D. deflexus</i> <i>aobifidus</i> — <i>uniformis</i> subzones		' <i>A. suecicus</i> '	<i>D. cf. hirundo</i>	<i>G. sino- dentatus</i>	<i>G. austro- dentatus</i>	Southwest China ⁷		
? FAUNA 2	FAUNA 3a		FAUNA 3c + 3d		graptolitic gap		FAUNA 4	Western Australia ⁸			
<i>Adelograptus</i>	<i>C. flexilis</i> <i>P. archaicus</i>	?	<i>D. fillmorensis</i> <i>D. millardensis</i>	<i>Tetragraptus</i>	' <i>nitidus</i> ' ' <i>patulus</i> '	? gap	' <i>bifidus</i> '	Utah.	W. USA ⁹		
G	H	I	J	'K'	gap		<i>Orthidialla</i> L	Shelly Zones ¹⁰	North America		
CASSINIAN					VALHALLAN		WHITE — ROCKIAN	Stages ¹¹			
Catoche — like Bathyrid fauna		V1 a b c		V2 a b	V3 a b	V4 a b		Shelly zones	Spitsbergen ¹¹		
KIRTONRYGGEN FORMATION		VALHALLFONNA OLENIDSLETTA MEMBER			FORMATION PROFILBEKKEN MEMBER			Lithostrat- igraphy			
REGRESSION		TRANSGRESSION			REGRESSION		TRANS — GRESSION	EUSTATIC LEVEL ¹¹			

Fig. 2 Correlation of early Ordovician sequences, late Tremadoc to early Llanvnn. Note the gap in the Late Arenig record of many areas, especially in cratonic regions. References: 1, Berry (1960); 2, Thomas (1960); 3, Elles & Wood (1901-18), Jackson (1962); 4, Bouček (1973); 5, Monsen (1937); 6, Tjernvik (1960); 7, Mu *et al.* (1979); 8, Legg (1976); 9, Braithwaite (1976); 10, Ross (1951); 11, Fortey (1980b).

1. Late Bendigonian (late *T. fruticosus* Zone). The lower part of the Olenidsletta Member, certainly embracing the lower 20 m, has a rich fauna of later Bendigonian age (and equivalent to Berry's Zone 5, *T. fruticosus* three-branched). The earliest graptolite-bearing beds of the Olenidsletta Member contain a stout extensiform species which we have identified with *Didymograptus* (*Expansograptus*) *praenuntius*, which is most abundant in the *Phyllograptus densus* Zone in Sweden (Tjernvik 1960). The fauna in the succeeding black, flaggy limestone-shale is flattened, and is a typical later Bendigonian (Be 3-4) assemblage, including the three-branched and two-branched forms of *Tetragraptus fruticosus*, *T. serra* (large robust forms here), *T. quadribachiatus*, *Didymograptus* (*Expansograptus*) *extensus*, *D. (E.) similis*, *Goniograptus thureaui*, *Sigmagraptus crinitus*, *S. praecursor*, *Etagraptus tenuissimus*, *Dichograptus octobrachiatus* (abundant), several deflexed didymograptids, *Pseudophyllograptus angustifolius* subsp. nov. (see p. 247), *Clonograptus trochograptoides* and *Orthodichograptus robinsi*. The earliest pendent didymograptid occurs in this interval, *D. cf. meitanensis*.

This is a fauna exactly comparable with that from the type Bendigonian of Australia; indeed,

Sigmagraptus crinitus, *Clonograptus trochograptoides* and *Orthodichograptus* have not previously been recorded from outside Australia. Yet the presence of deflexed didymograptids of *D. v-fractus* and *deflexus* type is more like the British early Arenig, and Jackson (1962) records these species as typical of the earliest (*D. deflexus* Zone) strata in the Lake District.

2. Chewtonian–earliest Castlemainian (*D. 'protobifidus'* – *D. bifidus* Zones). This interval intergrades perfectly with the Bendigonian below, and accounts for the middle part of the Olenidsletta Member, from 30 m to 105 m from base. It is convenient to discuss the *D. 'protobifidus'* and *D. bifidus* Zones together because they also intergrade perfectly – the eponymous species change between their typical morphologies in an entirely gradualistic fashion (see p. 224). As a whole the interval is characterized by an abundance of 'tuning fork' didymograptids and true *Phyllograptus*. The latter is distinguished in this paper from *Pseudophyllograptus* – a genus found both below and above (*P. angustifolius* s. str.), but not, in Spitsbergen at least, in this middle part of the Arenig. A number of the Bendigonian species carry on through varying parts of this interval – *Tetragraptus serra* and *Didymograptus (Expansograptus) extensus* are examples – but others (e.g. *Dichograptus octobrachiatus*) are much rarer than in lower strata. In the earlier part of the interval (*D. 'protobifidus'* Zone) the following species are characteristic: *Didymograptus (Didymograptellus) 'protobifidus'*, *D. (D.) diapason*, *D. (D.) cf. exilis*, *Phyllograptus typus*, *Tetragraptus amii*, *Laxograptus irregularis*, *Dichograptus octobrachiatus*, *Xiphograptus elongatus*, *Acrograptus gracilis* and the peculiar early *Isograptus*, *I. scandens* sp. nov. (p. 257).

The *D. bifidus* interval is typically developed between 75 and 90 m from base of the Olenidsletta Member, with gradation downwards into the '*protobifidus*' Zone. The same interval includes a short-lived shallowing event in the deposition of the Olenidsletta Member, which produced a drastic change in the trilobite faunas compared with those above and below, including the disappearance of the varied olenid trilobites with which abundant graptolites are normally associated in Spitsbergen. This change in facies may account for a general scarcity of graptolites through this interval, but a few horizons are productive. Typical species include: *Didymograptus (Didymograptellus) bifidus*, *Phyllograptus typus*, *Tetragraptus phyllograptoides triumphans* subsp. nov. (p. 200) and *T. reclinatus reclinatus*. In the upper part of the interval there is a horizon with the particular graptolites *Tetragraptus contrarius* sp. nov. (p. 213) and *Didymograptus (Didymograptellus) multiplex* sp. nov. (p. 229) together with *T. pseudobigsbyi*. The upper few metres of the interval contain little except *Pseudophyllograptus angustifolius chors* subsp. nov. (p. 244), *Tetragraptus phyllograptoides triumphans* and *Pseudotrigranograptus* in rather coarsely crystalline limestones. These beds are transitional in lithology and trilobite faunas between the nileid facies below and the olenid facies above, and the faunal changes in the benthic elements have been described in detail (Fortey 1975b: fig. 4). *Pseudotrigranograptus ensiformis*, with four thecal series, slightly precedes a species with three thecal series (*P. minor*, described by Fortey, 1971, as '*Tristichograptus ensiformis*').

It is a curious fact that the *D. bifidus* Zone (*sensu* Berry, 1960) is not recognized in certain of the Pacific Province sections (e.g. New Zealand, Cooper 1979; Idaho, Carter & Churkin 1977). As noted above, its presence in Spitsbergen is associated with a short-lived shallowing event in the otherwise olenid trilobite facies of the Olenidsletta Member. In the more oceanic facies, such as those represented in the Idaho and New Zealand sections, its place appears to be taken by a short interval in which *Isograptus victoriae lunatus* is a common species. No *Isograptus* species occurs within the *D. bifidus* Zone in Spitsbergen: this may be a case of facies control, because *Isograptus* species are known both above and below in the olenid facies. The *bifidus* interval in Spitsbergen is overlain by large populations of *I. victoriae victoriae*, and is thus equivalent to the lower part of the Castlemainian Stage, Ca 1, of Australia, and lower *I. v. lunatus* Zone of New Zealand.

3. Later Castlemainian (*Isograptus victoriae victoriae* – *I. v. maximus*). This interval, equivalent to part of Berry's (1960) *Isograptus* (8) Zone, comprises the upper 40 m of the Olenidsletta Member. Previous studies on the Spitsbergen graptolites (Fortey 1971, 1976;

Archer & Fortey 1974) have been concerned mostly with species from this part of the section. As a whole it marks a return to the deep, oxygen-poor conditions to which the olenid trilobites were adapted, such as was the case for the Bendigonian–Chewtonian interval of the lower Olenidsletta Member. The fauna of the upper part of the Olenidsletta Member includes the following species: *Xiphograptus formosus svalbardensis*, *X. patulentis*, *X. ?cypselo*, *Tetragraptus reclinatus toernquisti*, *Didymograptus (Expansograptus) cf. pennatulus*, *Kinnegraptus* sp., *Isograptus victoriae victoriae*, *I. victoriae cf. maximus* and *Dichograptus maccoyi densus* subsp. nov. (p. 186). The age determination of the fauna is well founded; there are none of the elements of typical Yapeenian assemblages such as *Isograptus divergens* or the *Oncograptus–Cardiograptus* group. Some of the *I. victoriae* specimens appear to bear incipiently manubriate proximal ends, but there is no evidence of true *Pseudisograptus* in the Olenidsletta Member.

Berry's (1960) Zone 8 of *Isograptus* was a rather coarse division, and the upper Olenidsletta fauna represents only the early half of that zone. As far as Cooper's (1973) zonation in New Zealand is concerned the fauna fits into the upper half of his *Isograptus victoriae lunatus* Zone, the earlier part of which is equivalent to our *D. bifidus* interval. *Pseudotrigrionograptus* occurs with a *D. hirundo* Zone fauna in Norway (see p. 250), and the same genus (both triserial and quadriserial) has been recovered by one of us (R.A.F.) from a high Arenig, probably *D. hirundo* Zone, fauna in south Wales, while Jackson (1962) records *P. ensiformis* from the *D. hirundo* Zone in the Lake District (but not from below that zone). If the first appearance of this highly distinctive graptoloid, one of the few distinctive species at this horizon, can be taken as a simultaneous event, then the base of the *D. hirundo* Zone should lie just above the first appearance of *Isograptus victoriae victoriae*. The first appearance of true biserial graptoloids occurs in the same zone in some sections. In south-west China (Mu *et al.* 1979) the first *Glyptograptus*, *G. sinodentatus*, occurs immediately below *Pseudotrigrionograptus* (which is there associated as usual with *G. austrodentatus*) and in that area it is the *Isograptus* species which are apparently absent.

4. Late Castlemainian–Yapeenian. The passage upwards into the Profilbekken Member marks a general shallowing, and the graptolites become progressively rarer. The lowest part of the Member has yielded good specimens of *Isograptus victoriae maximus* and *I. caduceus imitatus* (see Fortey 1976), together with *Pseudotrigrionograptus minor*, so that presumably the base of the Member is still within the top of the Castlemainian and the Member itself passes upwards into the Yapeenian. The Arenig–Llanvirn boundary lies somewhere within the considerable thickness of the Profilbekken Member. The occurrence of *Paracardiograptus* ? at 65 m from the base of the Member may indicate a horizon as young as the *Paraglossograptus tentaculatus* Zone (Llanvirn); from the same horizon come fragmentary robust stipes like those of a reclined tetragraptid species such as is found in the Ningkuo Shale of China and Yapeenian of Australasia. Green shales at the very top of the Profilbekken Member yield many specimens of *Tetragraptus cf. isograptoides*, also known from the Ningkuo Shale. Trilobite evidence (Fortey 1980a: 13–14), itself rather indirect, suggests that the best placing for the Arenig–Llanvirn boundary would be between the two successive shelly faunas of the Profilbekken Member (*V_{4a}* and *V_{4b}*). The graptolite material, so far as it goes, is not inconsistent with such a placement.

General history of Arenig graptolite faunas, Pacific province

A few general comments on the history of Arenig graptolite faunas in the Pacific Province are given here. As will become apparent from the systematic section below, many of the problems in the dichograptoids are nomenclatorial ones, but it is still possible to recognize certain broad features (Fig. 3) of the succession of Arenig graptolites throughout the Pacific Province if such nomenclatural *minutiae* are disregarded. We stress that these generalizations apply to the Pacific Province only – the broad belt to either side of the Ordovician palaeoequator, extending from North America, Greenland and Spitsbergen through the Tamir Peninsula, north-east

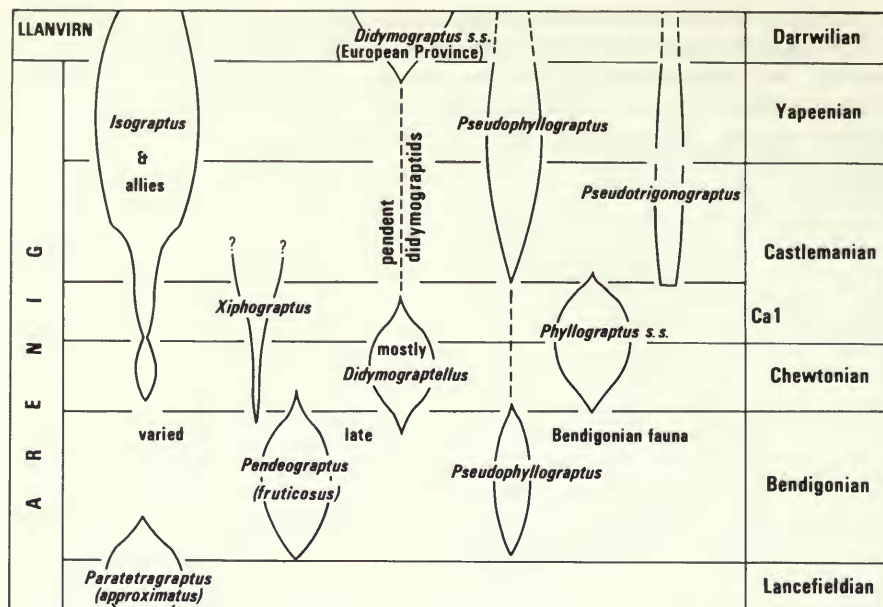


Fig. 3 Sequence of main dichograptoid groups in the Pacific Province. Although based mainly on dominance (relative abundance) it also reflects diversity in a general way.

Siberia, south-west China, to Australia and New Zealand. There is evidence that the sequence of events may have been different in areas – such as southern and central Europe – which were at higher latitudes in the early Ordovician.

1. The *Tetraraptus* (*Paratetraraptus*) radiation

The widespread occurrence of the H-shaped rhabdosomes of *Tetraraptus* (*Paratetraraptus*) *approximatus* and allied forms has been recognized for a long time (e.g. Skevington 1963). Although several species are involved, the abundance of these forms is stratigraphically limited to the earliest Arenig, although it has to be added that there is no proof of equivalent strata in the type Arenig of Wales. It seems reasonable to suppose that *Tetraraptus* (*Paratetraraptus*) is a monophyletic group. The Spitsbergen Arenig graptolitic succession begins too late to record this early radiation.

2. Phyllograptid history

In this paper we report the discovery that the phyllograptid grade of rhabdosome organization was reached by (at least) two different pathways. True *Phyllograptus*, based on the type species *P. typus* (Hall), has a fundamental structure quite different from the phyllograptids of 'angustifolius' type described by Bulman (1963a). The latter (*Pseudophyllograptus* n. gen.) is in essence a scandent *Tetraraptus*, whereas the true *Phyllograptus* has a complex internal structure which perhaps could not have been derived from a normal dichograptoid at all. From a stratigraphical view the important point is that true *Phyllograptus* spp. are confined to an interval within the Middle Arenig in Spitsbergen, and, so far as we can judge from descriptions based on flattened material, elsewhere in the Pacific Province. We have found no convincing example of true *Phyllograptus* from the Atlantic Province. *Pseudophyllograptus*, usually recorded as *P. angustifolius*, occurs both below and above the *Phyllograptus* interval (which corresponds to the *D. protobifidus*–*bifidus* Zones), and it is possible that rhabdosomes of this organizational type were derived from *Tetraraptus* on two occasions. In this connection it is of interest that we have discovered a *Tetraraptus* of *phyllograptoides* type below our upper *Pseudophyllograptus*, and considerably younger than *T. phyllograptoides* from Scandinavia,

which underlies the earlier *Pseudophyllograptus* burst. Several species of true *Phyllograptus* have been described by Mu *et al.* (1979), and again their stratigraphical distribution is consistent with what happens in Spitsbergen.

3. Pendent didymograptids

These somewhat intractable graptolites have generated a disproportionate amount of attention in the literature, because of an earlier belief that their main diversification occurred the world over in the early Llanvirn. This is not so. It has become apparent that there were two such events: one in the earlier Arenig, and again near the Arenig–Llanvirn boundary. In the Pacific Province, these episodes with pendants are separated by a stratigraphic gap, in which no pendent graptolites at all have been discovered: this corresponds to the interval, Castlemainian (Ca 2–3) and Yapeenian, well demonstrated by the upper part of the Olenidsletta Member in Spitsbergen. This disappearance of pendent forms is apparently sudden in Spitsbergen, and there seems no preservational cause to explain it. Part of the reason for the miscorrelation of the Arenig and Llanvirn pendent-bearing intervals was a scarcity of single sections in the Pacific Province spanning *both* radiations; two such have now been described, from Utah (Braithwaite 1976) and south-west China (Mu *et al.* 1979). In the latter the variation of rhabdosome form in the Arenig pendent didymograptids matches that usually associated only with the Llanvirn interval – broad, *D. munchisoni*-like, species are present, for example. We also have a few of these forms in Spitsbergen. Our discovery of isograptid development in one of the Arenig forms, and its inferred presence in others, contrasts with the *artus* type development of described Llanvirn species.

The combination of Arenig pendent didymograptids with *Phyllograptus*, *s.s.*, makes the Chewtonian – early Castlemainian interval a highly characteristic one. It forms the ‘filling’ between highly diverse later Bendigionian faunas below, and the main *Isograptus* radiation above. It would provide a natural way of discriminating a Middle Arenig from Lower and Upper Arenig intervals.

4. *Pseudotrigonograptus*

This distinctive genus has species with either three or four series of thecae. It is assuredly monophyletic, and so we do not have the kind of problems that have been encountered with *Pseudophyllograptus*, where the same grade of rhabdosome organization can be acquired in two or more lineages. As far as we can tell from the literature its first appearance is with or immediately before that of *Isograptus victoriae victoriae*, in sections containing both forms, and since the place of the latter within the evolving *Isograptus* plexus is now well known it is reasonable to conclude that *Pseudotrigonograptus* appears at about the same time in all sections. It is often found with *Didymograptus hirundo* (see p. 165), and it may be a reliable guide fossil for the correlation of that zone. It also always postdates the abundant record of *Phyllograptus*, *sensu stricto*.

5. *Isograptus*

The evolutionary history of species of *Isograptus* from Australasia was documented in detail by Cooper (1973), and it is encouraging for their use in correlation that the sequence of species in Spitsbergen is consistent with their occurrence in the southern hemisphere. The only modification to Cooper's account is the discovery of an early species (*I. scandens* sp. nov.) which anticipates within a single population some of the changes which were later undergone by the isograptids as a whole. Some individuals of *I. scandens* have become effectively scandent. Nonetheless, it remains true that the isograptids remain limited in abundance and variety until the mid-Castlemainian, when they commonly dominate assemblages on certain bedding planes. This expansion in numbers is coeval with the appearance of *Pseudotrigonograptus* and the disappearance of pendent forms commented on above. One might speculate that the isograptids, which are morphologically ‘reversed tuning forks’, somehow filled the ecological role vacated by the preceding *Didymograptus* (*Didymograptellus*) species.

6. *Xiphograptus*

One of the more surprising aspects of the isolated graptolites from the Spitsbergen Arenig was the discovery that there is a group of extensiform 'didymograptids' which are in fact more closely related to *Phyllograptus*, *sensu stricto*, than to other extensiforms of the subgenus *Didymograptus* (*Expansograptus*); these are placed in our new genus *Xiphograptus* (p. 289). The new genus is present as a relatively minor element in early Arenig extensiform faunas, the familiar, widely-recorded species of Hall (*extensus*, *patulus*, *similis*, etc.) all being dichograptids of normal (*Expansograptus*) developmental type. But at least as far as the faunas from Spitsbergen are concerned, *Xiphograptus* spp. are the numerically dominant extensiforms in the mid-Castlemainian. Whether this is more general in the Pacific Province is not known, because very well preserved material is needed to discriminate *Xiphograptus* from other extensiforms, but it is suggestive that identical or closely related species are an important element in the latest Arenig faunas of Utah as well (Braithwaite 1976). Spitsbergen and Utah are some 5000 miles apart today, and probably a similar distance apart in the Ordovician; with this known spread, there seems to be no reason in principle why *Xiphograptus* should not have traversed the entire Ordovician equatorial great circle, like many of the other Pacific Province forms.

Summary

The Arenig Series of the Pacific Province is divided into three broad stratigraphical divisions on graptolite faunas:

1. Lower Arenig. *T. approximatus* Zone at base, extending upwards to the diverse, Late Bendigonian faunas of the *T. fruticosus* Zone.

2. Middle Arenig (Chewtonian and Ca 1). Arenig radiation of pendent didymograptids probably referable to *Didymograptus* (*Didymograptellus*), accompanied by true *Phyllograptus* of *typus* type, and allied species. An abundance of very slender sigmagraptines (*Sigmatraptus*, *Laxograptus*, *Acrograptus gracilis*) also appears to be characteristic.

3. Upper Arenig (Ca 2–3, Ya). Pendent didymograptids apparently absent; appearance of *Pseudotrigonograptus* and reappearance of *Pseudophyllograptus*; main isograptid radiation, and probably also that of *Xiphograptus*. Appearance of dipleural scandent graptolites.

The most fundamental division is between the Middle and Upper Arenig as defined here; many of the genera which were to dominate mid-Ordovician faunas probably have their roots in late Arenig species. The Arenig–Llanvirn boundary is not related to so profound a change in the graptolite faunas as that between the Middle and Upper Arenig as defined here: a renewed burst of pendent didymograptids is typical especially in the European Province, but the diplograptid, isograptid and glossograptid history in the Llanvirn is a continuation of that in the Upper Arenig.

Relation to trilobite faunas

Fortey (1980a) summarized the succession of the trilobite faunas through the Valhallfonna Formation. More than 100 species of trilobites have now been described from this formation, and the coexistence of such rich faunas, possibly the richest of this age anywhere, with varied graptolitic faunas is one of the reasons for the exceptional importance of the Spitsbergen Ordovician sequence. Fortey divided the Valhallfonna Formation into four major divisions (V_1 to V_4) from bottom to top, the boundaries between which marked changes in biofacies associated with particular suites of trilobite genera (Fortey 1975b). Within any one of these divisions, biostratigraphically significant assemblage zones in the same facies were designated by suffixes (V_1a , V_1b . . . etc.). The change from V_3 to V_4 at the boundary between the Olenidsletta and Profilbekken Members marks the beginning of the progressively shallowing sequence that closes Ordovician sedimentation in this area. These trilobite faunas can now be accurately calibrated against the graptolite ranges (Fig. 1, p. 160). In general the trilobites permit a somewhat finer division of the Valhallfonna Formation. On the other hand, so many of

the trilobites, particularly the olenids, are not known elsewhere that the correlation potential of the benthic trilobite assemblages is at the moment limited. However, this does not apply to certain pelagic trilobites, such as *Carolinites* and *Opipenter*, species of which are very widespread. These pelagic trilobites spread into areas without graptolites, and thus permit correlation between shelly faunal zones, such as those of Ross (1951) and Hintze (1953), and the graptolitic sequence in which they occur in Spitsbergen. This correlation has been described in some detail by Fortey (1976) and need not be repeated here, but the conclusions are summarized in Fig. 2 (p. 163).

Valhallan Stage and the late Arenig regression

One of the consequences of the correlation of the relatively deep-water Spitsbergen succession (up to V₄b) with platform sequences described from many sites in North America (Fortey 1980b) is the recognition of what appears to be a shelly faunal gap in these sequences below the earliest recognized Whiterock faunas (represented by V₄b in Spitsbergen) and above the highest recognized Canadian strata (V₂b in Spitsbergen). This was termed the Valhallan Stage (Fortey 1980a) and includes the succession of shelly faunas V₃a–b, V₄a.

In graptolitic terms the Valhallan can now be shown to be equivalent to the Ca 2–3 interval plus all or part of the Yapeenian, that is, with the important Upper Arenig interval described above (and probably equivalent to the British zone of *Didymograptus hirundo*). Fortey (1980b) indicated that the reason why the Valhallan shelly fossils are missing over much of platform North America was a regression below the Arenig–Llanvirn boundary, and suggested that this might prove to be so widespread as to imply a eustatic cause. If this were so its effects should be seen on what were separate plates in the Ordovician. We would predict that in epicratonic graptolitic sequences, where the regression would also produce seaward displacement of epieric facies, the characteristic *Isograptus victoriae victoriae* – *maximodivergens* fauna would be missing; true oceanic facies would, of course, be little affected. The following evidence suggests that the eustatic explanation may be the correct one.

1. In Australia Legg (1978) has described the stratigraphy of the Canning Basin, a peripheral cratonic succession with a mixed trilobite–graptolite fauna. His Fauna 3 contains a number of graptolites in common with the Spitsbergen succession, including typical representatives of the late Bendigonian and, above, pendent didymograptids and what is probably true *Phyllograptus*, indicating the presence of the ‘*protobifidus*’–*bifidus* interval. The succeeding Fauna 4 contains a wealth of biserial graptoloids, and other species which indicate a correlation with the Darriwilian. Thus there is a ‘gap’ in the succession of zones corresponding to the regression, and members of the typical *Isograptus* radiation are absent. Lithologies in the upper part of Fauna 3 tend to be limestones or sandstones, where Fauna 4 is accompanied by shale deposition.

2. In south-west China, according to the account of Mu *et al.* (1979), there is a richly fossiliferous equivalent of the *bifidus*–‘*protobifidus*’ interval, with what is without doubt true *Phyllograptus*, many pendent species, and a peculiar local radiation of deflexed forms. The pendent-bearing interval is followed by a zone of ‘*Azygograptus suecicus*’ with variable populations of *Azygograptus* and *Phyllograptus*, some of the latter of which are almost certainly true *Phyllograptus* and not *Pseudophyllograptus*. The following zone of *D. cf. hirundo* is very impoverished in species, and those that are present are mostly curious, endemic many-branched species of *Schizograptus* and *Mimograptus*. The zone that follows (*Glyptograptus sinodontatus*) marks the appearance of *Pseudotrigrigonograptus* in these Chinese sections, with the first biserial graptoloid, and this is followed by strata of undoubtedly Llanvirn age with the second flowering of pendent didymograptids, accompanied by a diverse selection of biserial forms. Thus there is an interval through which pendent species are absent, and there is no evidence at all of the isograptids so typical of oceanic sequences in the late Arenig. The regressive phase is probably accommodated in the zones of *D. cf. hirundo* and *G. sinodontatus*, and possibly that of ‘*Azygograptus suecicus*’ as well. In contrast to the Canning

Basin there are strata representing the interval, but these have a peculiar and endemic fauna, which we would regard as probably adapted to the inner shelf conditions of the shallower phase. True oceanic species (*Isograptus* and allies) were absent, but gradually return during the following transgressive phase, heralded by *Pseudotrigrionograptus*. It is noted that the stratigraphic columns of Mu *et al.* (1979: opp. p. 12) show the appearance of limestones in otherwise shaly sections at the Zone of '*Azygograptus suecicus*'.

3. In Utah Braithwaite (1976) described the graptolite sequence from an outer cratonic site where trilobite-bearing rocks are often interbedded with greenish graptolitic shales. The lithology of these shales is unlike that of typical black, fissile graptolitic shales of 'geosynclinal' type. Again, our Middle Arenig interval is certainly present, with what is probably true *Phyllograptus* associated with pendent didymograptids showing isograptid development, and therefore referable to *Didymograptus* (*Didymograptellus*). Pendent graptoloids reappear in the Llanvirn Kanosh Shale. Between the two pendent-bearing intervals lie the Wahwah and Juab Limestone Formations. The younger of the two, the Juab Limestone, has only two species of graptolites, and one of these (identified with *Didymograptus nitidus* (Hall) by Braithwaite) has a described development which shows it to be a *Xiphograptus* species. Furthermore other extensiform didymograptids with development described by Braithwaite from the upper Wahwah Limestone Formation would now be classified in *Xiphograptus*; a form occurring just below the Juab Limestone, incorrectly described as *D. extensus* by Braithwaite, may be identical to *Xiphograptus formosus svalbardensis* (Archer & Fortey) from Spitsbergen. Finally, what is identified as *Phyllograptus anna* (Braithwaite 1976: 32–35), which occurs with the *formosus*-like species, is clearly a *Pseudophyllograptus* from its development, a genus that makes its reappearance above the *D. bifidus* interval in Spitsbergen. So there seems to be some evidence of a very thin interval at the top of the Wahwah Limestone representing the Upper Arenig. No isograptids are present at all. There may still be a considerable disconformity between the Wahwah and Juab Limestones but the graptolite faunas of the latter are not sufficient to resolve this problem. The trilobites from the Juab are of Hintze's (1953) Zone L, which we have good reason (Fortey 1980a: 13–15) to correlate with the basal Whiterockian V_{4b} (youngest) trilobite fauna from Spitsbergen. Hence the entire Valhallan interval has to be accommodated within the upper 17 m of the Wahwah Limestone, compared with virtually a third of the Valhallfonna Formation in Spitsbergen. By comparison with zones above and below it would be very attenuated, and this too would be consistent with the idea of a Valhallan regression.

These three examples have been discussed in detail because they occur in areas which were on three different plates in the early Ordovician, and which were clearly affected simultaneously by an event in widely separated parts of the Pacific Province. What happened in each area is consistent with the idea of the Valhallan regression. Note that faunas in true oceanic sites were unaffected by the regression. For example in the oceanic facies contemporaneous with the Wahwah and Juab Limestones, now in the allochthonous Vinini Formation (Ross & Berry 1963) of Nevada, there is a good succession of *Isograptus* species. Spitsbergen appears to be unique in recording a rich, mixed shelly/graptolitic fauna across this interval in the Bathyrud trilobite Province.

The same event should have affected the Atlantic Province, but the more indirect basis for correlation should always be considered first. Nonetheless there is evidence of a similar event at a similar time. For example, the 'Orthoceras Limestone' interval between the Lower and Upper *Didymograptus* Shales in the Oslo region falls exactly where we would expect our regressive phase. Furthermore the fauna described by Spjeldnaes (1953) from the top of the Lower *Didymograptus* Shale at Slemmestad includes both *Didymograptus hirundo* and *Pseudotrigrionograptus* (see p. 250). In south Wales work in progress by R.A.F. and R. M. Owens shows that there is a change in facies at the Arenig–Llanvirn boundary which introduces a number of relatively shallow water trilobite genera, such as *Ectillaenus*, in light-coloured shales, into a sequence otherwise dominated by black mudstones and turbidites, with 'open ocean' trilobite faunas.

Rhabdosome morphology, development and terminology

The terminology currently used in graptolite description has evolved over many years. The early work of Hall (1858, 1865), Lapworth (1873, 1875) and Nicholson & Marr (1895) was refined by Elles & Wood (1901–18), who evolved a terminology which was used by almost all subsequent workers and which forms the basis of that used today. Detailed morphological studies of rhabdosomes isolated from their matrix late last century (Holm 1890, 1895, Wiman 1895, 1901) and this century (Kraft 1926, Bulman 1932–36a, 1944–47, Kozłowski 1949, and several papers during the last two decades) has led to a refinement or revision of many terms used to describe the morphology, structure and development of the rhabdosome, together with the addition of many new ones. Bulman (1955, 1970) has systematized terminology in the *Treatise* and provided the basis for terminology used in the present work.

Throughout this paper, the term **dichograptoid** is used as an informal term to describe graptolites with dichograptid grade of organization, but without phylogenetic connotations.

It was perhaps inevitable that the renewed attention here directed towards the proximal region of the dichograptoid rhabdosome should result in the necessity for a revision of Bulman's scheme of terms to describe the proximal end. In view of the importance here attached to development type, mode, and proximal structure it is proposed to isolate these three concepts and redefine them. The new morphological information now available has required a revision and redefinition of Bulman's classic sequence of development types and their supposed phyletic relationships. For much the same reason it is proposed to revise Bulman's system of thecal notation, and a reference frame for orientation of the rhabdosome is proposed, together with a system for stipe notation.

Developmental types and their nomenclature

Systematic study and classification of the various kinds of early astogenetic structure and development have been very largely the work of Bulman. He incorporated the work of earlier authors, particularly Holm (1890, 1895), Wiman (1893, 1895) and Elles (1922), with his own studies of Swedish etched specimens prepared by Holm into a scheme of 'progressive changes in the proximal end of the graptolite rhabdosome' (Bulman 1932 and, somewhat revised, 1936b, 1970: fig 49). His scheme of development types incorporated not only thecal budding sequence but also structural features of the proximal region, such as directions of growth of proximal thecae and their arrangement with respect to the sicula.

The term 'proximal development type' is here used to refer only to the sequence of budding of proximal thecae. Among Graptoloidea, the first two, three, four or more thecae may alternate in origin by progressive postponement of formation of the first dicalycal theca of the rhabdosome. In dichograptoids the dicalycal theca is either $th1^1$ (Fig. 4c; dichograptid type of Bulman) or $th1^2$ (Fig. 4a–b; isograptid type of Bulman). The diplograptids, not part of this study, are here considered briefly since any overall scheme of development types must incorporate them. In the early forms theca 2^1 is dicalycal but in many later forms the dicalycal theca is some later theca or else dichotomy never takes place at all and thecae alternate throughout the rhabdosome (aseptate forms). For purposes of the present discussion, we recognize two types among diplograptids; in the first (diplograptid 1) $th2^1$ is dicalycal (Fig. 4d); in the second ('diplograptid 2', which itself probably includes several distinct types) the dicalycal theca is $th2^2$ or a later theca, or the rhabdosome is aseptate. The four development types are listed in Table 1. Uniramous forms such as *Azygograptus* and *Monograptus* are thought to have been derived from biramous forms by loss or suppression of the initial dichotomy, and may warrant recognition as a discrete development type.

Development of the dichograptoid rhabdosome has been examined in detail by Cooper & Fortey (1982) and related to the early astogenetic development of dendroids. The dichograptid type of development, in which theca 1^1 is dicalycal, was found to be rare among dichograptoids and largely confined to pendent didymograptids of the *D. artus* group of Llanvirn age. The name dichograptid type therefore seems inappropriate. Furthermore it comprises a single stage, based on the Welsh *Didymograptus 'bifidus'*, known as the *bifidus* stage. However,

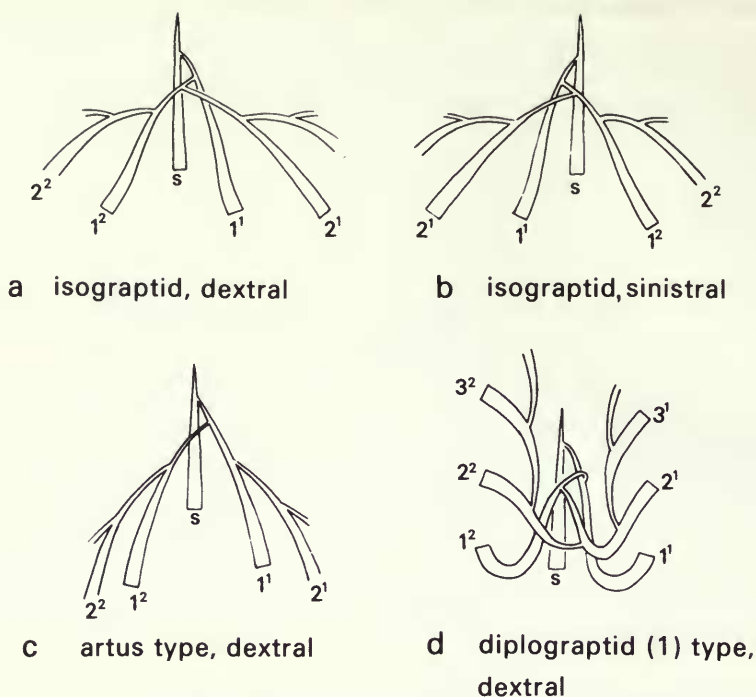


Fig. 4 Thecal diagrams to illustrate the terms *dextral*, *sinistral*, *right-handed* and *left-handed*. a, Isograptid development type with right-handed origin of $th1^2$ (and left-handed origin of 2^1) dextral mode of development (e.g. *Didymograptus (Expansograptus) extensus*). b, Isograptid development type with left-handed origin of $th1^2$ and sinistral mode of development (*Isograptus caduceus imitatus*). c, artus development type with right-handed origin of $th1^2$ and dextral mode of development (*Didymograptus artus*). d, diplograptid (1) development type with left-handed origin of $th1^2$ and dextral mode of development (*Glyptograptus austrodentatus*).

Didymograptus bifidus, *sensu stricto*, is here shown to have $th1^2$ dicalycal, and the Welsh 'bifidus', with dicalycal $th1^1$, represents a different species requiring a new name. The name **artus type** has therefore been proposed to replace dichograptid type and is used in this work.

All stages in which $th1^2$ is dicalycal are collectively referred to by Cooper & Fortey (1982) as the isograptid type of development, which is found to be dominant among the dichograptoids. The leptograptid type of Bulman (1970) with dicalycal $th1^2$ was synonymized with the

Table 1 Development types proposed here compared with those of Bulman (1970).

Dicalycal theca	Development types proposed here	Development types of Bulman (1970)
$th1^1$	1. artus	{ 1. dichograptid (<i>bifidus</i> stage) 2. pericalycal (Glossograptina)
$th1^2$	2. isograptid	{ 3. isograptid (<i>minutus</i> , <i>extensus</i> and <i>gibberulus</i> stages) 4. leptograptid
$th2^1$ $th2^2$ or later	3. diplograptid (I) } 4. diplograptid (II) }	5. diplograptid

isograptid type and the *minutus* stage was also referred to the isograptid type following Bulman (1970).

The various stages within the two main development types found in dichograptoids, which were thought to represent a progressive series by Bulman (1936a, 1955), have received decreasing emphasis in recent years as it has become increasingly unlikely that they represent transitional stages in the evolution of the isograptid from the dichograptid type as originally proposed (Bulman 1932, 1936a). In 1970 Bulman suggested that the two main types stood in parallel rather than serial relationship and that there is little purpose in attempting to distinguish the various stages within each type. In any case, the morphology of the rhabdosome rarely allows them to be determined with precision. Most recently, the isograptid type of development of the rhabdosome is claimed by Cooper & Fortey (1982) to be the primitive type for all Graptoloidea and to have been derived directly from the Dendroidea by suppression of bithecae. The *artus* and diplograptid development types, on this hypothesis, must therefore have been derived from forms in which theca 1² is dicalycal. An ancestor with isograptid development has long been suggested for the earliest diplograptids by Bulman (1936a: 94, text-fig. 30) and more recently by others (e.g. Jenkins 1980). In this paper we suggest that the Llanvirn pendent didymograptids of the *artus* group were derived from an Arenig pendent form with isograptid development.

In summary, we recognize two types of development in dichograptoids; the *artus* type and the isograptid type. No stages are distinguished.

Proximal structure and its nomenclature

The second concept employed in Bulman's classification of the various kinds of proximal development is the growth directions and arrangement of proximal thecae, here referred to as 'proximal structure'. The distinction between the leptograptid and isograptid types of Bulman (1970: fig. 49), assuming that the leptograptid type has th1² dicalycal, is essentially based on the horizontal, rather than downward, growth of proximal thecae. Thus it is based on proximal structure, rather than on development type as defined here. In terms of development type, we regard it as identical with the isograptid type. There is great variety in proximal structure which, among the dichograptoids at least, holds much hope for deciphering phylogeny.

The terms streptoblastic and prosoblastic (Bulman 1963) refer to features of proximal structure, as do the terms pericalycal and platycalycal (Bulman 1968). The 'pericalycal type' of development was the term used by Bulman (1970) for the Glossograptina, which have th1¹ dicalycal and a pericalycal arrangement of proximal thecae. We would regard the glossograptines as of *artus* development type and with pericalycal structure. In fact, any of the other types of development would tend to impede the formation of pericalycal structure. However, reassessment of the glossograptines in the light of Finney's (1978) comments is needed.

The terms right- and left-handed refer to features of proximal structure and need clarification. They were first introduced by Stubblefield (1929) for describing the development of *Adelograptus hunnebergensis* and *Clonograptus tenellus*: 'One of the primary stipes may cross the sicula, either to the right or to the left-hand side, the sicula [in reverse aspect] is then for purposes of description termed respectively, right- or left-handed'. Right- and left-handed are commonly used to indicate the origin of the dicalycal theca (e.g. Bulman 1932: 5; 1970: V33, V75), for other proximal thecae (Bulman 1970: 77), or simply for 'development of the early thecae' (Bulman 1963a: 276). It should be noted, however, that Bulman used the terms in the sense opposite to that of Stubblefield, i.e. right-handed to Stubblefield was left-handed for Bulman, who sometimes used 'biologically left-handed' to make the distinction clear. It is in Bulman's sense that the terms have come to be accepted.

The terms do not necessarily relate to the direction of growth and orientation of a theca but but may merely reflect its origin. Hence in dicranograptids and other forms with diplograptid (1) development type, the origin of theca 1² is left handed but it grows around th1¹ and across the sicula in a clockwise or dextral sense, in the same way as in dichograptids where the origin of this theca is right-handed.

Thus there is a need for two sets of terms relating to mode of development. **Right-** and **left-handed** are retained here to indicate the origin of a theca, that is whether it arises on the (biologically) right or left side of its parent theca. In the proximal part of the rhabdosome, this is determined (as used by Bulman) with respect to the sicula (Fig. 4), but after the first dichotomy it is determined with respect to the parent theca. Thus in *Phyllograptus typus* (Fig. 75, p. 282) the origin of theca 1² is right-handed (on th1¹), the origin of th3¹ is right-handed (on th2¹) and the origin of th3² is left-handed (on th2²). In normal budding along a stipe thecae originate on the dorsal side of their parent thecae, and the terms right- and left-handed are not applicable.

The terms dextral and sinistral are proposed to describe the sense of rotation of a theca which grows from one side of a bifurcation to the other and is independent of whether it is right- or left-handed in origin. **Dextral mode** of development indicates that the first 'crossing canal', the proximal part of theca 1², grows around in a dextral or clockwise sense with respect to the sicula; th1¹ will thus lie to the right of the sicula when seen in reverse aspect (Fig. 4a). This is by far the most common mode of development in graptolites. In the **sinistral mode** of development, th1² grows around in a sinistral or anticlockwise sense so that th1¹ lies to the left of the sicula in reverse aspect (Fig. 4b). Examples are few and include *Oncograptus* (Bulman 1936b), the Glossograptina, and *Isograptus imitatus* together with several dendroids (including *Dictyonema flabelliforme*, *Clonograptus tenellus*, and *Adelograptus hunnebergensis*; Stubblefield 1929) in which development mode appears to be arbitrarily sinistral or dextral. The terms can also be applied to subsequent dichotomies where a sense of torsion is imparted by the first daughter theca of a dicalycal theca and relates to the predicalycal theca. Thus in *Tetragraptus* (*T.*) *phyllograptoides triumphans* (Fig. 5a, b), and in fact all tetragraptids, the second order dichotomy on stipe¹ side is sinistral whereas that on the stipe² side is dextral.

Thecal notation

Bulman's (1936a: 32) system of trinomial notation for thecae in the proximal region of the rhabdosome was derived from the binomial nomenclature introduced by Elles (1897: 189–190)

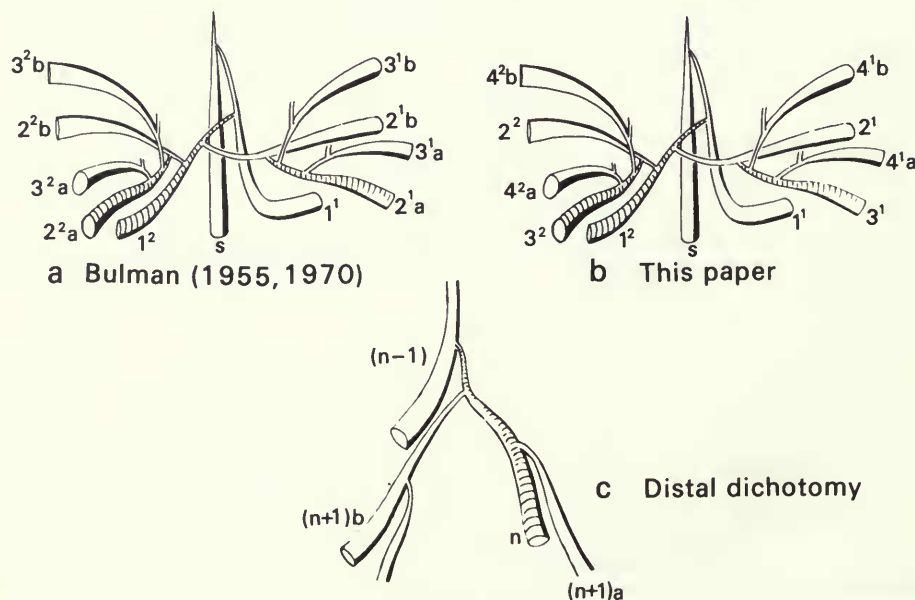


Fig. 5 Thecal diagrams to show budding sequence and thecal notation in proximal and distal regions of a branching dichograptid. a, Bulman's (1955, 1970) scheme for the proximal region. b, Scheme proposed in this paper for proximal region. c, Scheme for a distal dichotomy. Diagrams a and b are based on *Tetragraptus* (*T.*) *phyllograptoides triumphans* described in this paper, p. 201. Diagram c is based on *Dichograptid* sp. A of Skevington (1965). Dicalycal thecae striped.

and designed to accommodate those tetragraptid and phyllograptid rhabdosomes whose development was then known. The scheme used in the *Treatise* (Bulman 1970: V74) is basically the same one (Fig. 5a). In 1936, prior to the concept of the dicalyca theca, it was thought that the third-formed theca of the tetragraptid rhabdosome, $th2^1$ (and the fourth formed theca, $th2^2$) split equally into two; thus Bulman (1936a: 32) states that it 'divides and opens to the exterior as two separate thecae which are called $th2^1a$ (on the reverse side) and $th2^1b$ (on the obverse side)'. Although it was later realized that $th2^1a$, rather than being a sister theca to $th2^1b$, is in fact a daughter theca budded off from $th2^1b$ (Bulman 1955: fig. 39, 3; 1970: fig. 53), nonetheless the original nomenclature was retained. Thus the designations $th2^1a$, $th2^1b$ do not denote two daughter thecae of a dicalyca parent theca, but thecae whose apertural regions form part of stipes a and b respectively. The scheme thus reflects the position in a thecal series (stipe) of the apertural portion of a theca, rather than its strict order of budding. Theca 2^1b is the first theca of stipe 1b and the first theca of stipe 1a is the subsequently budded $th2^1a$ (Fig. 5a); $th3^1a$, 4^1a etc. are successively budded thecae of stipe 1a . Since thecae 1^1 and 1^2 do not form part of the second order stipes in the species studied by Bulman (*T. bigsbyi* and '*Phyllograptus angustifolius*') they needed no a or b connotation.

Bulman's system has the merit that thecae can be labelled from their position in a thecal series without knowing their budding sequence. Against this it can be said that thecal notation is used mainly where budding sequence is known, often to describe the budding sequence specifically, as in discussions of the various development types. In these instances it seems more logical that nomenclature should reflect the budding sequence rather than the position in the stipe. The budding sequence is certainly a more fundamental and conservative character than the position a theca holds in a stipe, and the system fails for such forms as *Phyllograptus*, *sensu stricto* (here defined to exclude '*Phyllograptus angustifolius*', = *Pseudophyllograptus* gen. nov.) where the initial two thecae, $th1^1$ and 1^2 , form the first thecae of stipes 1a and 2a respectively rather than lying medially between them as in *T. bigsbyi* and *P. angustifolius*.

A further, and possibly more serious, objection to the present system lies in the difference in notation used for proximal and distal dichotomies. It is claimed elsewhere (Cooper & Fortey 1982) as a general rule that in branching dichograptoids, division of the stipe in distal dichotomies is achieved by a repetition of the process by which division takes place in the proximal region, i.e. of the initial development. If this rule holds, it is obviously desirable that the one notation system should be applied at all dichotomies. The current notation of thecae of a distal dichotomy differs from that used for thecae of a proximal one, as a comparison of Bulman's (1970) figs 64.1 and 64.2 shows.

It is therefore proposed to change to a system which reflects the sequence of thecal budding and to use it for proximal development and for all subsequent dichotomies. In the new system the daughter thecae of a dicalyca theca, $th\ n$, are labelled $(n+1)a$ and $(n+1)b$. In the original system, 'a' was used for stipes (and thecae) developed on the reverse side of the rhabdosome and 'b' for stipes on the obverse side. Although this scheme has proved to be generally satisfactory it could not be applied to distal dichotomies of rhabdosomes in which the proximal region is not preserved. It is therefore proposed to denote the second budded theca (and subsequent stipe) of a dicalyca parent, 'a', and the first budded theca, 'b', consistent with the earlier system. The old and new systems of nomenclature are given for the thecal diagram of *Tetragraptus* (*T.*) *phyllograptoides triumphans* in Fig. 5a, b. By extension, the scheme can be applied to subsequent dichotomies, e.g. a dicalyca theca 4^1a would produce daughter thecae 4^1a^1 and 4^1a^2 , and so on. For isolated distal fragments (Fig. 5c), a dicalyca theca n produces first a daughter theca $(n+1)b$ which gives rise to stipe b and next a second daughter theca $(n+1)a$ from which stipe a is derived, that is, the notation shown in Bulman's (1970) fig. 64.1 for a distal fragment of *Dichograptid* sp. A of Skevington (1965).

When we turn back to the proximal region and examine the notation of thecae of the initial dichotomy, that giving rise to the two primary stipes, we find that the first- and second-formed thecae are labelled 1^1 and 1^2 respectively. If the new scheme were applied to these they would be relabelled $th1$ and $th2$ and the superscript 1 and 2 would be introduced only for the daughter thecae of the first dicalyca theca, $th1^2$ (or 1^1 in *artus* type development), and their descendants.

Such a change would alter the nomenclature of all subsequent thecae and make the comparison of the old and new systems difficult and confusing. It would also require revision of the schemes used for diplograptids, dicranograptids, etc., now so well established in the literature, and generate an unwarranted upheaval in conventional usage. It is therefore proposed to leave notation of the first dicalyca theca, and its parent theca in the case of isograptid type developmental forms, as at present and introduce the new notation from the second dicalyca theca(e) onwards. For species with *artus* type development there is no change in nomenclature.

Later astogenetic development – dichotomy and branching types. In classification of multi-stiped dichograptoids much weight has been placed in the past on branching patterns and the number of terminal stipes. In discussing the multistiped forms from Spitsbergen, particularly those of the subfamily Sigmagraptinae nov., we have found it useful to discuss branching pattern in terms of the spacing and distribution of dichotomies throughout the rhabdosome. A number of descriptive terms have proved necessary.

Dichotomy is the process by which a stipe divides to produce two new stipes. All dichotomies appear to employ the same process of division, described by Cooper & Fortey (1982) as the isograptid type of stipe division. Dichotomies can be consecutive throughout the rhabdosome or delayed. In *consecutive dichotomies* only one theca separates successive dicalyca thecae and there is thus only a single theca between each branching node. Examples are *Tetragraptus bigsbyi* and *Dichograptus octobrachiatus*. In *delayed dichotomies* two or more thecae separate successive dicalyca thecae and branching nodes are thus more spaced out. A good, if somewhat exaggerated, example is *Laxograptus* [*Zygograptus*] *irregularis* redescribed here, p. 270.

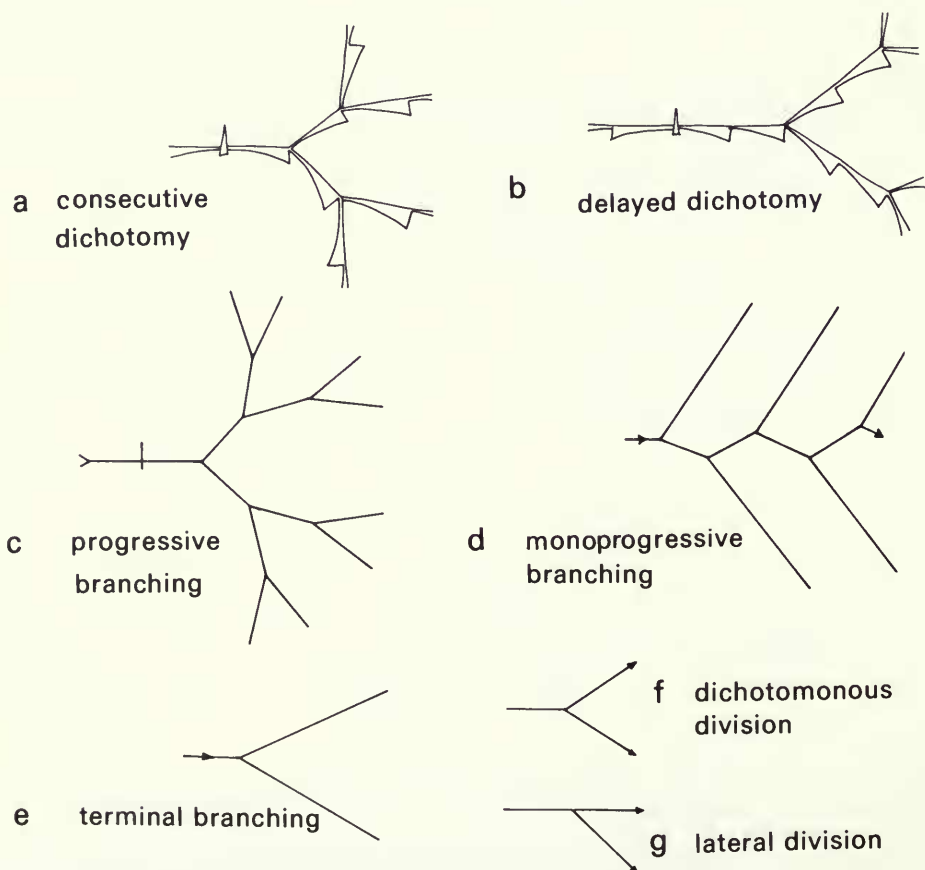


Fig. 6 Branching types and their nomenclature as followed in this paper.

Branching is of several kinds. *Progressive branching* is that kind in which two new branches are formed, each of which subsequently divides again. In *monoprogessive branching*, two branches are formed only one of which further divides, the other remaining undivided. Branching in *Loganograptus* and *Dichograptus*, for example, is of the progressive kind, whereas branching in *Goniograptus*, *Sigmagraptus*, *Pterograptus* and *Trichograptus* is of the monoprogessive kind. The term *terminal branching* can be used when neither of the two new branches further divides and they thus become terminal stipes of the rhabdosome. However, in discussion, it is often convenient to regard terminal branching as of the same kind as, but the final stage of, whatever branching type precedes it.

Two further terms are already in use and defined in the *Treatise* (Bulman 1970) and relate to the angle of divergence of the daughter stipes. *Dichotomous branching* is used where the two daughter stipes diverge symmetrically from the parent stipe and *lateral branching* where one daughter stipe continues the direction of growth of the parent stipe whereas the other diverges from it at an angle. The terms are a little unfortunate in that we now believe that both lateral and dichotomous branching are produced by normal dichotomy (i.e. by the isograptid type of stipe division) and both are, in that sense, dichotomous.

Stipe notation

Stubblefield (1929: 274 and footnote) extended his use of right- and left-handed to denote the primary stipes of *Clonograptus tenellus*, *Adelograptus hunnebergensis* and, by extension, any rhabdosome with a proximal dichotomy. However, a less ambiguous notation, derived from Elles' (1897) binomial thecal notation, has gained wide acceptance and is in general use today (e.g. Bulman 1970). It can be extended to denote stipes of the second, third, fourth, etc., orders by use of polynomials as shown in Fig. 7 and derives logically from thecal nomenclature. It should be noted that where a dichotomy (after the first) is of sinistral mode, the left-hand stipe (seen from above) is denoted b (or ² depending on the order of dichotomy) and the right-hand stipe is denoted a (or ¹). Where a dichotomy is of dextral mode the left-hand stipe is denoted a (or ¹) and the right-hand stipe b (or ²). Where mode of dichotomy is unknown, notation of the daughter stipe is arbitrary.

The term 'stipe' strictly speaking refers to a segment between dichotomies but it is convenient to leave definition of the term deliberately loose and to rely on context for precise meaning. The notation scheme provides a means for precise identification of individual segments. We see no reason why the one scheme cannot be applied to both lateral and dichotomous division since we regard both as resulting from the one, isograptid, branching process and thus to be of the same fundamental type.

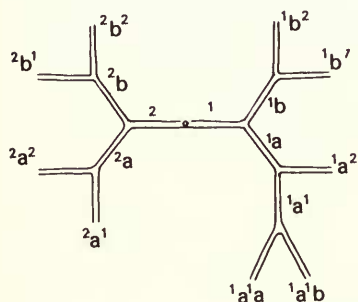


Fig. 7 Notation of stipes in a multistiped rhabdosome.

Orientation of the rhabdosome

It is useful, for purposes of description, to have a frame of reference for orientating the rhabdosome. The terms *dorsal* and *ventral*, *proximal* and *distal* are well established in reference to individual stipes, to individual thecae and to the rhabdosome itself. Terms for describing stipe attitude are also well known (Bulman 1970: fig. 38), but there appears to be no generally accepted overall frame of reference as has been established in other biological groups.

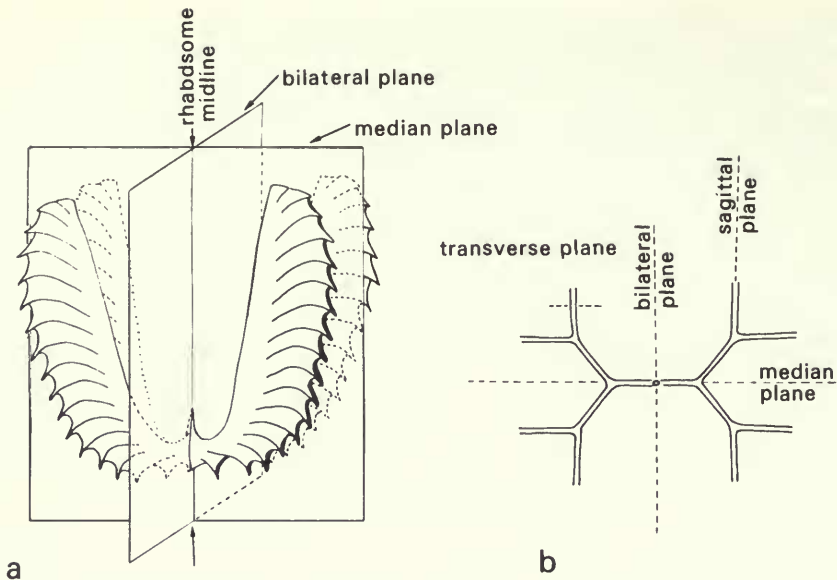


Fig. 8 Planes of reference of the rhabdosome. a, *Tetragraptus pseudobigsbyi* with the two principal planes of symmetry. b, a multistiped dichograptid (dorsal view) with planes of reference and symmetry.

The scheme proposed here (Fig. 8a, b) is primarily for convenience in description of the Didymograptina of Bulman (1970), but most of the suggested reference planes and axes can be applied to other suborders and to the Anisograptidae. Most dendroids, however, with their irregular branching characteristics and rhabdosome habit, defy attempts to impose planes, or axes, of symmetry on them.

For descriptive purposes the rhabdosome is usually orientated with the apex of the sicula (and nema) uppermost. The rhabdosome *midline* (the primary axis of symmetry) passes through the sicula and medially through the rhabdosome, from top to bottom (Fig. 8a). The plane containing the rhabdosome midline and the two primary stipes is here called the *median plane* of the rhabdosome; it is a plane of symmetry in rhabdosomes developed on both the didymograptid (and tetragraptid) and triograptid planes. In diplograptids it passes through the ventral midlines of the two thecal series whereas in Glossograptina it passes between the two thecal series themselves. The plane which lies normal to the median plane, and which also contains the rhabdosome midline, is the *bilateral plane* of the rhabdosome – the principal plane of symmetry in bilateral rhabdosomes. The third plane of reference, of course, is already referred to as the *horizontal plane*. The long axis of a stipe is generally referred to as the *stipe axis*; the plane normal to the stipe axis is here called the *transverse plane* of the stipe and the plane passing through the dorsal and ventral margins of the stipe, and containing the stipe axis, is here called the *sagittal plane* of the stipe. In Diplograptina, the sagittal plane coincides with the median plane of the rhabdosome and in many monograptids (*M. turriculatus*, *Cyrtograptus*) is the only plane (besides the horizontal plane) that can readily be applied.

Stipe expansion diagrams. We have used this method as a simple and graphical way of directly comparing different specimens and species of dichograptoids on a single diagram. It is more objective than the general statements about the form of stipes, rate of expansion and change in thecal length found in many descriptions. The graphs plot the width of a stipe, from its dorsal margin to the tip of the apertural denticle, against the thecal number (1, 2, 3 . . .) counted from the proximal end (Fig. 9).

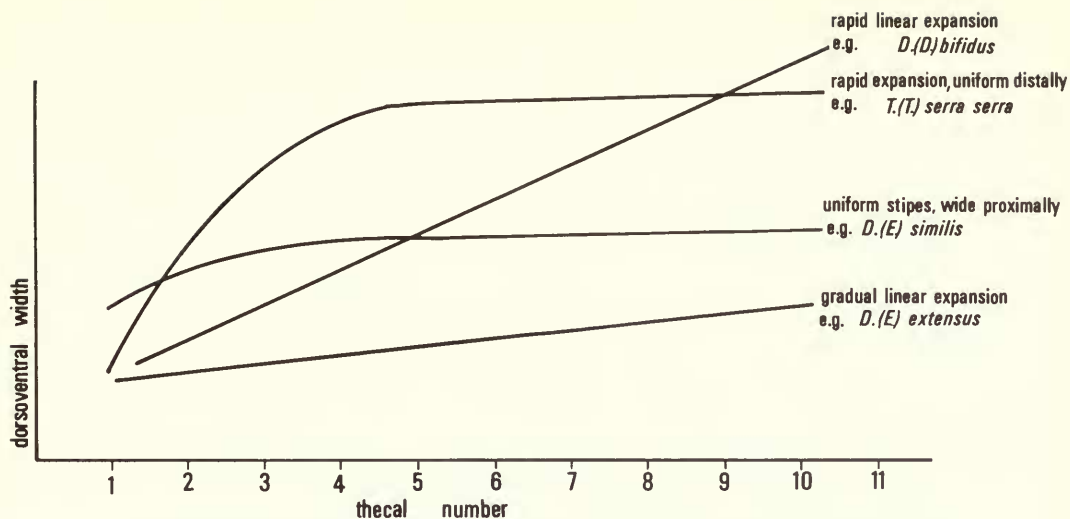


Fig. 9 Stipe expansion diagram with some characteristic expansion curves.

Different species within a given form genus tend to have characteristically different shapes on the stipe expansion diagrams. Variation can be simply assessed by plotting stipes from several specimens in a population on the same diagram. We have found this method of particular use in evaluating the specific status of rather undistinctive species of the subgenera *Didymograptus* (*Expansograptus*) and *Didymograptus* (*Didymograptellus*). In general the shape of the expansion curve tends to be rather constant within a species, but the absolute value of, for example, maximum stipe width can be highly variable (see *Tetragraptus serra serra*, p. 196). The method has the advantage that the shape of the expansion curve can still be deduced when some thecae are poorly preserved and when the vagaries of preservation make some individual thecae relatively wide or narrow. Some species have growth increments which result in regular expansion diagrams to which a straight line regression may be fitted with correlation coefficients in excess of 0.9. For the sake of clarity it is often easier to compare sets of such regression lines derived from a population of rhabdosomes, although the intercept does not necessarily correspond with the proximal width of the stipe. Non-linear growth is typical of other species, and the general shape has been emphasized using a flexible curve to 'average' the points. Note that this method includes no measure of thecal density, usually recorded as number of thecae corrected for 10 mm: in theory it is possible to get identical expansion diagrams from two species with very different thecal spacing. Once proximal end characters, general thecal and rhabdosome form, and thecal spacing have been described, the expansion diagram neatly encapsulates many of the features of the distal stipes, and facilitates direct comparison of type series with specimens to hand.

Other terms

Most other terms used are already in general usage but the following need clarification. *Growth lamelli* and *growth lines* both refer to overlapping half-rings (fusellar rings or fuselli) of the periderm and are visible in transparent isolated rhabdosomes. Much of the isolated material from Spitsbergen is too heavily carbonized to be rendered transparent by bleaching but nonetheless shows fine striations on the outer surface of the rhabdosome which can be traced under camera lucida and indicate the growth directions of thecae. Although the striations proved to be always parallel with fuselli, where both could be observed, the spacing of the striations was found to be twice as close as that of fuselli (e.g. in *Xiphograptus formosus svalbardensis*). It is important therefore to distinguish them from true fuselli and they are here called *growth striations*. They are extremely useful for determining growth direction and

development of the proximal region, for example in *Phyllograptus typus*, but do not necessarily represent individual increments in the fusellar tissue.

Another term we have found useful refers to the arch formed by the ventral walls of $th2^1$ and $th1^2$ in the isograptid development type. It is usually a conspicuous feature and a good guide to isograptid type development even in strongly flattened material. It is here called the *isograptid arch*. The symmetrical arrangement of the sicula and first theca, characteristic of isograptids and approached by many species with isograptid development, is referred to as *isograptid symmetry*, following Cooper (1973).

The term **fornix** refers to the arched strut which stands in place of the interthecal septum in the axial region of *Phyllograptus*. The wide opening between thecal series is termed the **fornical foramen**.

Unless otherwise specified stipe width and thecal width are measured in the sagittal (dorso-ventral) plane.

Principles of dichograptoid classification

There appears to be a degree of consensus in the papers of graptolite workers over the last few years that the only satisfactory classification of the group will be one based on their inferred phylogeny (Rickards, Hutt & Berry 1977; Bouček 1973). The historical problem has been that the genera or families originally proposed for graptolites have often been based on the grade of organization of the rhabdosome, especially the number and arrangement of stipes. In a series of papers Bulman (e.g. 1936a, 1963, 1970) has argued that in many cases the particular grade of organization found in a graptolite rhabdosome may be polyphyletically derived. The 'genera' in use were often stratigraphically useful in a crude way, and had the advantage of being readily recognizable, but may include clusters of species whose closest relatives lie not within the same form-genus, but in some other form-genus of an equally polyphyletic nature. But over the last three decades various other genera have been proposed (on our estimate perhaps half of those used in the 1970 *Treatise*), which are explicitly defined in terms of characters of presumed phylogenetic significance – they are believed to be 'true' phylogenetic concepts in which every species included in the genus is presumed to be more closely related one to another than to any species in another genus, and to be all derived from a common ancestor. Thus, for example, *Aulograptus* Skevington 1965 is of *Didymograptus* grade of organization, but defined as a phylogenetic unit by having climacograptid thecae. This leaves graptoloid classification in an unsatisfactory, hybrid state. The progress towards solution of some of these problems was well put by Bulman & Rickards (*in* Bulman 1970: 150) in discussing monograptids: . . . 'the hope remained that from the portmanteau genus . . . various soundly based genera could progressively be extracted as investigation of different species provided the opportunity'. The important phrase here is 'soundly based'. The recognition of the polyphyletic nature of some of the long-used graptolite genera has led to the proposal of new 'genera' by some authors which are every bit as polyphyletic as their more encompassing predecessors.

This problem is nowhere more acute than in the dichograptoids (= Dichograptidae of Bulman 1970). Bulman (1955) suggested the different phylogenetic routes by which a rhabdosome of *Tetragraptus* or *Didymograptus* organizational grade could be derived. His diagrammatic representation would suggest that not only are most dichograptoid genera polyphyletic concepts, but also that the family as a whole is probably polyphyletic – it is the taxonomic expression of a stratigraphically-based anagenetic grade of evolution, meaning little more than the statement 'early graptoloids tend to have several stipes'.

There have been a number of attempts to define phylogenetically meaningful groups in the dichograptoid plexus. Mu (1957) erected a family Sinograptidae for a number of genera paralleling the dichograptoid 'genera' on stipe number and attitude, but united by a presumed shared, derived character (strong prothecal folds) which reveals an underlying phylogenetic connection. Most graptolite workers would probably accept that the Sinograptidae is a phylogenetic entity. As far as the old form genera like *Didymograptus* and *Tetragraptus* are concerned several genera have been proposed to split up these large assemblages of species. In

Didymograptus there are four such – *Expansograptus* Bouček & Přibyl 1951, *Corymbo-graptus* Obut & Sobolevskaya 1964, *Acrograptus* Tzaj 1969 and *Aulograptus* Skevington 1965. The first three of these are simply formal upgradings of Elles & Wood's (1901) informal division of *Didymograptus* based on stipe attitude. There is little to suggest that this is genuinely a phylogenetically important character, and there is evidence to suggest the contrary. For example, we describe a group of extensiform graptolites in this paper (p. 289) which on stipe attitude definition should belong to *Expansograptus* or *Acrograptus* but which have a proximal end structure which shows them to be unrelated to the type species of either of these 'genera'. The proximal end structure serves to define a phylogenetic entity, but within this group stipe forms vary from extensiform (i.e. *Expansograptus*) to strongly declined (i.e. *Acrograptus*), which shows how mutable such general characters can be (and the same plasticity is shown by the sinograptids). The indications are, then, that the current definition of subgroups within the old genus *Didymograptus* would introduce the possibility of more polyphyly – in effect, would compound the traditional problem. The exception is *Aulograptus*, which as has been said has a derived character (climacograptid thecae) which is probably not polyphyletic. However, the other names are validly proposed, and we here employ them where appropriate as subgenera of the form-genus *Didymograptus*, based on the characters of their nominated type species, of which stipe attitude is not regarded as specially important. Particular problems associated with this procedure are given in the systematic treatment (pp. 218, 231, 239). The same arguments can be repeated for the subdivision of the form-genus *Tetragraptus*. In all these dichograptoids the phylogenetic validity of a genus depends on the recognition of a character or characters which may reasonably be supposed to indicate its monophyly (synapomorphy). Too little is known of detailed dichograptoid structure from isolated material to make more than a start in the direction of phylogenetically-defined genera.

There are no invariable rules about which characters shall be taken as signifying phylogenetic connections above the species level. However, we are clear in our assertion that the characters of the proximal end, particularly the sicula and first three or four thecae, are important in the discrimination of monophyletic groups. This can be justified both from a theoretical standpoint, and in the light of our own experience with isolated material.

1. It is reasonable to regard astogeny – the development of the colony – as a special case of ontogeny. Gould (1977: 269) implicitly makes this assumption in his discussion of thecal elaboration, and the same principle is accepted in coral and bryozoan work. From a phylogenetic standpoint the early astogeny may be treated in a broadly similar way to the embryological history of the single organism, and will be subject to von Baer's 'laws of development' (Gould 1977: 56). This is not to assert that the proximal development was immune from natural selection – the fact that fundamental changes in proximal structure do occur shows that this was not so – only that graptoloids *sharing distinctive proximal end characters will belong to a monophyletic group*.

2. Another way of showing this is to demonstrate that the same grade of rhabdosome organization may be reached by two independent lineages and that this independent origin can only be revealed by studying the proximal end characters. The proximal end structures in this case are homologous, whereas the rhabdosome structure as a whole is a parallelism. The phyllograptid rhabdosome is an excellent example. At first sight the four-stiped, scandent habit may seem peculiar enough for its monophyletic origin to be certain. Yet we show here that there are two totally different proximal structures with mature phyllograptid habit. One of these, that described by Bulman (1936a), is consistent with other dichograptoids. The other is different from most dichograptoids, but can be compared with a group of species with extensiform didymograptid habit (here put in *Xiphograptus* gen. nov.), typified by a short sicula with a long virgellar spine, and an antivirgellar origin of th1¹. There are only two possibilities:

(a) that the phyllograptid habit is the phyletic character and the proximal end structure independently derived, or

(b) that the proximal end structures are indicators of phyletic relationships, and the phyllograptid habit independently derived.

If we adopt the first we have to accept the extremely unlikely proposition that at an early stage of growth, *before* the defining character of the rhabdosome has been initiated, two quite different but closely related free-living growth stages have no close phyletic relationship with identical growth stages of other graptoloids. If the second explanation is accepted, then the only concession that has to be made is to allow the phyllograptid rhabdosome organization to be polyphyletic, in the same way as scandency in general, or periderm reduction. The second alternative is favoured, indeed Bulman (1936b: 44) suggested that '*Phyllograptus*' could have arisen on several 'lines of descent' although for reasons different from those put forward here.

Families and subfamilies

If the basis of classification outlined in the previous section is acceptable, it provides a method for the identification of natural groups above the genus level. For example true *Phyllograptus* and *Xiphograptus* are more closely related one to another than to any dichograptid since they share distinctive proximal characters. Hence in terms of proximal structure the family Phyllograptidae of Lapworth, 1873, should contain these two genera, but exclude the superficially comparable *Pseudophyllograptus*. This definition of the family Phyllograptidae contrasts with that of Mu (1957) who included both *Phyllograptus*, *sensu lato*, and *Pseudotrigranograptus*, on the basis of their multiseriate scandent habit.

Similarly, within the Dichograptidae it should be possible to define groups of genera (subfamilies) with comparable proximal end structure, which may span the whole gamut of stipe number and arrangement. Sigmagraptinae subfam. nov., we suggest, is one such grouping, and others should be identifiable when more isolated material has been described. We cannot accept the elevation of the old 'form genera' *Didymograptus*, *Tetragraptus*, etc., to family status, such as has been used by Mu *et al.* (1979), because this is simply an upgrading of the old polyphyletic classification. Such units have little to recommend them stratigraphically, and nothing to recommend them phylogenetically.

Ultimately the dichograptid subgroups, and the Phyllograptidae, should 'root back' into the Anisograptidae. We see it as inevitable that, at least for the time being, the Anisograptidae should be retained as a paraphyletic stem group for subsequent graptoloid evolution, although much is likely to be gained from detailed studies of anisograptid development to detect the beginnings of those features which were to characterize the main lines of graptoloid evolution in the Arenig and younger rocks.

Systematic descriptions

Order **DENDROIDEA** Nicholson, 1872

Genus **CLONOGRAPTUS** Hall, 1873

TYPE SPECIES. *Graptolithus rigidus* Hall 1858.

Clonograptus trochograptoides Harris & Thomas 1939

Pl. 2, fig. 2

STRATIGRAPHIC RANGE. Lower part of Olenidsletta Member, V₁b, 22 m from base, early Arenig, late Bendigionian.

MATERIAL. PMO NF2792, NF2795.

DISCUSSION. This very robust *Clonograptus* species was originally described from Bendigionian rocks in Australia, and this is its first record other than the description of the type by Harris & Thomas (1939). No other Arenig *Clonograptus* (e.g. *C. flexilis* Hall) has so short and dense proximal branching, except *C. norvegicus* Mønst. 1937. In that species the dichotomies are very irregular, and rather appear to give rise to a series of subordinate stipes from major, thicker stipes (Mønst. 1937: pl. 20); the habit is generally lax and flexuous. Our specimen does not attain the size of the holotype figured by Harris & Thomas, but in our experience

Clonograptus can be variable in the ultimate number of dichotomies, and there seems to be no reason to suppose any specific difference in this case.

Order **GRAPTOLOIDEA** Lapworth, 1875

DISCUSSION. Classification above the generic level used here differs from that adopted in the *Treatise* (Bulman 1970) in several respects. The Family Dichograptidae is redefined using characters of the sicula and early development in combination with rhabdosomal features. It comprises three subfamilies, Dichograptinae, Isograptinae and Sigmagraptinae, discussed below. The new definition of Dichograptidae excludes those forms which have a virgellar spine on the sicula and in which theca 1' originates and grows on the antivirgellar (dorsal) side of the sicula, namely the genera *Phyllograptus* Hall, *sensu stricto*, and *Xiphograptus* gen. nov. These two genera are here grouped in the family Phyllograptidae Lapworth 1873.

Other families that appear to be phylogenetically well based have been mentioned in our discussion of the principles of dichograptid classification, and include Sinograptidae Mu 1957 and Abrograptidae Mu (*in* Mu & Lee 1958). Discussion of the relationship between all these families at higher level, and classification between the ranks of family and order, is beyond the scope of this paper. The informal term 'dichograptoid' is used for convenience in discussion for Dichograptidae + Phyllograptidae, i.e. the Dichograptidae of Bulman 1970.

Family **DICHOGRAPTIDAE** Lapworth, 1873

DIAGNOSIS (revised). Development platycalcal, of isograptid or, rarely, *artus* type, and dextral or, rarely, sinistral; virgellar spine not present on sicula, theca 1' originates and develops on ventral side of sicula; rhabdosomes generally have bilateral symmetry; all dichotomies employ isograptid division; dicalcal thecae throughout rhabdosome are separated, in budding succession, by one or more unicalcal thecae; dichotomies consecutive or delayed, branching progressive or monoprogressive; stipes usually uniserial, rarely biserial, triserial or quadriserial. Thecal form usually simple, rarely of climacograptid type.

DISCUSSION. Bulman's (1959, 1970) division of the Dichograptidae into the sections Gonio-grapti, Temnograpti, Schizograpti, Dichograpti, Tetragrapti and Didymograpti was a polyphyletic generic grouping of convenience – revealed clearly in his diagram (1970: fig. 75) showing suggested phylogenetic relationships among some dichograptid genera. In admitting the arbitrary nature of the sections, he stated (1970: V104) that 'no satisfactory subdivision of the large and varied family Dichograptidae on a formal subfamilial basis is yet possible.' It is our belief that although morphological information on the structure and development is lacking in many genera, we now know enough to make a start on regrouping species and genera into units that can reasonably be said to have a phylogenetic basis.

We here recognize three subfamilies – Sigmagraptinae n. subfam., Isograptinae Harris 1933, and Dichograptinae Lapworth 1873 – the phylogenetic rationale of which is discussed under the appropriate systematic headings below.

Subfamily **DICHOGRAPTINAE** Lapworth, 1873

DIAGNOSIS (provisional). Sicula generally relatively short, curved distally so that apertural region is commonly brought into phase with thecae of stipe²; development generally isograptid but usually lacking isograptid symmetry; *artus* type development rare; dichotomies from one to many or lacking altogether.

DISCUSSION. We retain for the time being the Dichograptinae as a polyphyletic taxon including several genera (*Tetragraptus* and *Didymograptus*, *sensu lato*) which are still not definable in phylogenetic terms. For reasons stated above (p. 180) we do not accept the upgrading of these genera into higher taxa (e.g. Mu 1958, Mu *et al.* 1979) as this merely compounds the problems in defining natural groups. In the present work proximal end structure is regarded as important in the discrimination of taxa at subfamily level or above, and branching patterns alone – for

example, the number of terminal stipes – are considered to be more subject to problems of parallelism.

Dichograptinae in the strict (phylogenetic) sense should be based on the proximal end structure of *Dichograptus* itself. The development of *D. octobrachiatus* was illustrated by Braithwaite (1976: pl. 10, figs 4–6). It is typified by a sicula about 1.5 mm in length. Theca 1¹ originates in the prosicula and grows considerably longer than the sicula; it diverges from the ventral side of the sicula, at the level of the sicular aperture, exposing about half the total length of its ventral wall. Theca 1² grows to similar proportions on the other side of the sicula; the two initial thecae thus form a symmetrical pair on either side of the sicula. Development is of isograptid type and dextral mode, as shown in Braithwaite's (1976) fig. 6B. Subsequent branching appears to be much like that of *T. serra* (p. 201) and *T. reclinatus* (p. 204) as described in this paper. The proximal region has a characteristic appearance with the small 'tooth' of the aligned distal part of the sicula midway between the apertures of th1¹ and th1². We can match this proximal type in several dichograptid species, as well as in the *T. serra* group of *Tetragraptus*. The structure is seen in *Didymograptus* (*Expansograptus*), *sensu stricto* (p. 231), and it would be surprising if it did not pertain in such genera as *Orthodichograptus* and *Schizograptus*. Together, these might form a phylogenetically-defined Dichograptinae. However, there are several problems which would make this premature. The type species of *Dichograptus* is the relatively slender species *D. sedgwickii*, the development of which is not described; we are uncertain of the relationship of the pendent and deflexed dichograptoids to this group; and there has to be a subfamily available to accommodate the many species with unknown development – dichograptids *sensu lato* – for which Dichograptinae is most appropriate.

For these reasons we adopt the concept of Dichograptinae *sensu lato* in this paper. Because of its polyphyletic nature, the above diagnosis is provisional. Although isograptid development greatly predominates throughout the group, isograptid symmetry is rarely achieved, providing a convenient means of distinguishing, for example, between reclined *Didymograptus* and the Isograptinae. In many didymograptids the sicula is curved so that the apertural region is deflected towards, and looks as if it is part of, stipe². However, the distal part of the sicula is commonly curved towards the stipe² side and its dorsal margin lies in contact with the ventral margin of th1²; its apertural region is thus brought 'into phase' with thecal apertures of stipe². The effect is generally less marked, however, than in the Isograptinae where the sicula and th1¹ grow to identical proportions and the distal portion of the sicula forms an integral part of stipe².

Genus *ORTHODICHOGRAPTUS* Thomas, 1972

TYPE SPECIES. *Orthodichograptus robbinsi* Thomas 1972.

Orthodichograptus robbinsi Thomas 1972

Fig. 10

STRATIGRAPHIC RANGE. Lower Olenidsletta Member, 20 m from base on Olenidsletta, early Arenig (late Bendigonian), V₁b.

MATERIAL. PMO NF2052.

DISCUSSION. *Orthodichograptus robbinsi* has hitherto been recorded only from its type locality near Bendigo, Victoria, Australia. A second occurrence of the type and only species is therefore of some interest. It is found in Spitsbergen with a latest Bendigonian assemblage, as it is in Australia. As Thomas (1972) remarked, it is essentially like *Dichograptus octobrachiatus* in structure, but develops additional dichotomies distally. Our specimen with proximal end is like the type specimens in proportions, although the central disc is not preserved in the impure limestone Olenidsletta lithology. Several of the stipes show the fourth-order branches. Fragments of larger specimens are associated with that showing the proximal end, and attest to the very large size reached by this species.

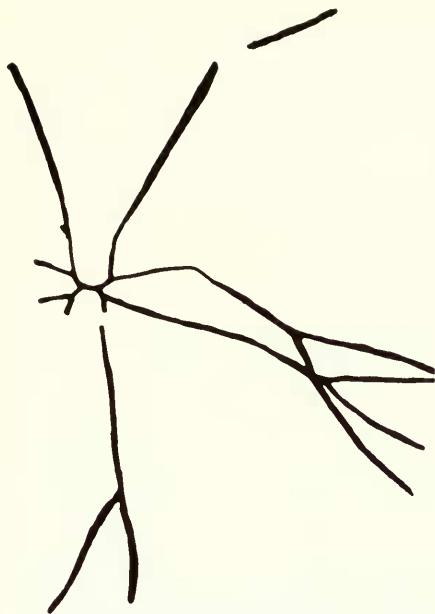


Fig. 10 *Orthodichograptus robbinsi* Thomas, PMO NF2052, 20 m above base of Olenidsletta Member on Olenidsletta; $\times 1$.

Genus *DICHOGRAPTUS* Salter, 1863

TYPE SPECIES. *Dichograptus sedgwicki* Salter 1863.

Dichograptus maccoyi maccoyi Harris & Thomas 1940

Fig. 11

1940 *Dichograptus maccoyi* Harris & Thomas: 129; pl. 1, fig. 1a–d; pl. 2, fig. 2.

non 1979 *Dichograptus maccoyi* Harris & Thomas; Cooper: 58–59, fig. 25; pl. 5f.

STRATIGRAPHIC RANGE. Lower part of Olenidsletta Member, 22 m from base, at top of Bendigonian faunas (early Arenig).

MATERIAL. PMO NF2796.

DISCUSSION. Harris & Thomas (1940) originally described this species from the Bendigonian of Victoria. Cooper's (1979) material is from a much younger horizon, and we can also recognize a younger form in Spitsbergen, which we here regard as different enough from *D. maccoyi maccoyi* to be accorded subspecific recognition (below). All the figures of Harris & Thomas

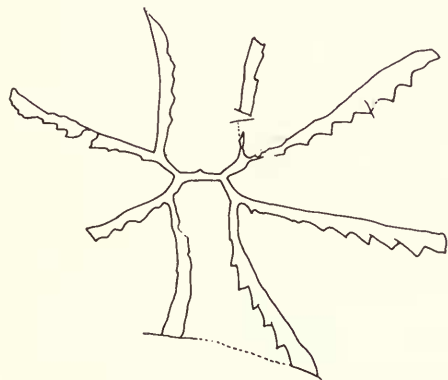


Fig. 11 *Dichograptus maccoyi maccoyi* Harris & Thomas, PMO NF2796, 20 m above base of Olenidsletta Member; $\times 3$.

show narrow stipes, 1.4 mm wide at most, and generally about 1.5 cm long. There is little indication of more than the gentlest curvature of the stipes when flattened in profile, and the species must, at most, have been only gently reclined. Thecal apertures are 1 mm apart or slightly more, giving a spacing of 9–10 in 10 mm. The length of the first- and second-order stipes is also close to 1 mm, which indicates that the early dichotomies happened at successive thecae. Our specimen agrees exactly with the original description, except that the stipes do not exceed 1 cm in length, a difference we do not regard as important.

Dichograptus maccoyi densus subsp. nov.

Fig. 12

1979 *Dichograptus maccoyi* Harris & Thomas; Cooper: 58–59, fig. 25; pl. 5f.

DIAGNOSIS. A subspecies of *D. maccoyi* with distinctly reclined stipes less than 1 cm long; thecal spacing 13–14 in 10 mm.

STRATIGRAPHIC RANGE. Upper part of Olenidsletta Member, V₃b, late Arenig, Castlemainian (Ca₂) (= *Didymograptus hirundo* Zone).

MATERIAL. **Holotype**, PMO NF3223; paratypes many specimens on NF3218, NF3220; NF3219.

NAME. 'Densely spaced.'

DESCRIPTION. Our most complete rhabdosome, the holotype, is about 1.5 cm across; none of the individual stipes are longer than 6 mm. The eight stipes show distinctly curved dorsal walls when flattened in profile, and it is certain that the rhabdosome was reclined after the proximal four-stipe stage. One small growth stage shows the sicula, preserved somewhat oblique to the primary stipes, slender, about 1.3 mm long. Funicle 1.8–2.5 mm long, usually preserved dorsal side uppermost, with a diameter of 0.25–0.3 mm; one specimen shows a thecal aperture almost on a level with the first dichotomy. Second-order stipes 1 mm long or slightly less, and enclosing an angle of 100°–120°, again presenting their dorsal aspect. The third dichotomy includes an acute angle (as seen in the flattened state) and the stipes are presented in profile. They widen rapidly over three or four thecae from 0.5 mm to 1.2 mm, and appear to maintain constant width thereafter. Thecae are inclined at about 40°. They present different included angles between the free ventral wall and the apertural margin according to the angle of flattening, but in true profile this angle is about 80°. Thecae are densely spaced, the distance between apertures about 0.7 mm, corresponding to a thecal spacing of 13–14 in 10 mm.

DISCUSSION. This species agrees closely with *D. maccoyi maccoyi* in its proximal end structure, and it seems appropriate to accord the differences subspecific rank only. However, the strong curvature of the stipes, their rapid widening to 1.2 mm, and the dense thecal spacing (13–14 in 10 mm as compared with 9–10 in 10 mm) are distinctive enough to place our population outside the nominate subspecies. Cooper's (1979) specimen from New Zealand, although from a slightly

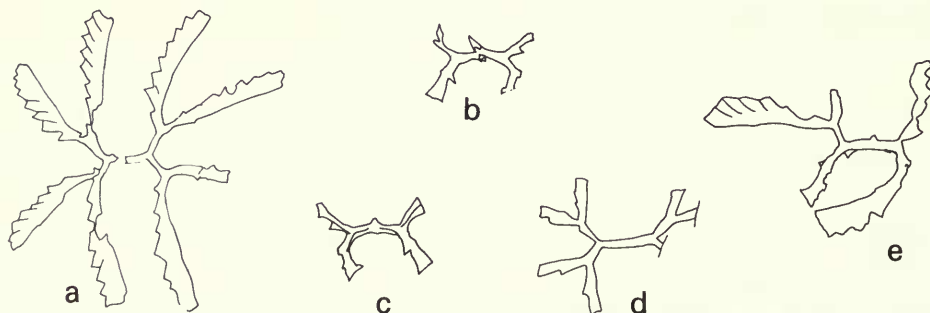


Fig. 12 *Dichograptus maccoyi densus* subsp. nov. a, PMO NF3223. **Holotype**. b, NF3218b. c, NF3220. d, NF3218a. e, NF3218. All from upper part of Olenidsletta member, 130 m above base; $\times 3$.

higher horizon, is closer to *D. maccoyi densus* than to *D. maccoyi maccoyi* with regard to thecal spacing. Of other slender *Dichograptus* species, that named by Harris & Thomas (1940) as *D. norvegicus* has straight stipes, with long, narrow thecae 8 in 10 mm distally, while *D. changshanensis* Mu 1957 has much more slender stipes, only 0.55 mm wide distally. There may prove to be a complete transition stratigraphically between *D. maccoyi maccoyi* and *D. maccoyi densus*. We have one small growth stage (NF1719) which may belong here, and which occurs midway between the two subspecies stratigraphically.

Dichograptus solidus Harris & Thomas 1940

Fig. 13

1940 *Dichograptus octonarius* var. *solida* Harris & Thomas: 129–130; pl. 1, fig. 3; pl. 2, fig. 4.

1979 *Dichograptus octonarius* J. Hall; Cooper: 59; pl. 5e; fig. 26.

STRATIGRAPHIC RANGE. Olenidsletta Member, V₁b and V₃, 21–116 m above base. Bendigonian to Castlemainian.

MATERIAL. PMO NF3359, NF3360.

REMARKS. The rhabdosome is formed by progressive branching to three orders of apparently consecutive dichotomy. Details of sicula and proximal structure unknown. First-order stipes are together 2 mm long, second-order stipes are about 1 mm long. Third-order stipes are about 20 mm long; they are curved, concave dorsally and are inclined to the bedding plane by rotation along their sagittal axis. Their original attitude in the rhabdosome appears to have been weakly to strongly reclined. Third-order stipes widen rapidly, reaching a maximum of at least 3 mm. Thecae are spaced about 9 in 10 mm.

The Spitsbergen specimens most closely match the reclined forms of *Dichograptus* from the Castlemainian and Yapeenian of Victoria figured by Harris & Thomas (1940: pl. 1, figs 2a–b) as *Dichograptus octonarius* Hall and *D. octonarius* var. *solida* Harris & Thomas. The specimen NF3359, with strongly reclined stipes, resembles that figured by Cooper (1979: fig. 26) from the Castlemainian of New Zealand and referred to *D. octonarius*. A reclined rhabdosome seems to have become regarded as characteristic of *D. octonarius*. Yet a reclined attitude of stipes was not mentioned by Hall and is not determinable in his single figured specimen from Levis; a 'pseudo-reclined' appearance in this specimen results from some stipes being folded over on themselves.

It therefore seems unwise to continue using Hall's name. The next available name for the reclined forms appears to be *Dichograptus solidus* Harris & Thomas 1940.

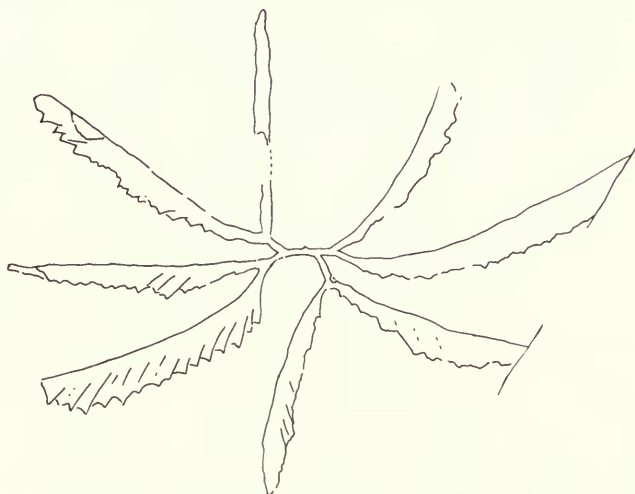


Fig. 13 *Dichograptus solidus* Harris & Thomas, PMO NF3360, 21–22 m above base of Olenidsletta Member; $\times 2$.

Third-order stipes in our specimens are slightly less broad than in those of the holotype figured by Harris & Thomas, a difference that may be partly or wholly accounted for by the fact that our stipes are twisted and do not present the full dorsoventral profile.

Dichograptus octobrachiatus Hall 1858

Pl. 2, fig. 3

STRATIGRAPHIC RANGE. Through most of the Olenidsletta Member, 10–105 m from base, spanning most of the Arenig (Bendigionian to Castlemainian), and V_1a – V_3 . Abundant only in the late Bendigionian part of the section.

MATERIAL. Includes PMO NF828, NF4171, SM A105817–8 and many others.

DISCUSSION. Material from Spitsbergen is flattened, and adds little to previous information about this widespread species. Proximal end development appears to have been like that of *Tetragraptus serra*, described in detail here (p. 195), and the mature rhabdosome results from progressive branching, by consecutive dichotomies, to the third order. The last dichotomy of some second-order stipes is suppressed resulting in six- or seven-branched rhabdosomes, which are not uncommon in our late Bendigionian assemblages. Distal stipes are straight, which is the main difference from *D. solidus*. Length of 'funicle' is 2 mm, and secondary stipes 1.0–1.5 mm. Distal stipes reach 4.5 mm in width (including projecting flattened thecal apertures 0.5 mm long), but stipe width on most specimens is 3–3.5 mm. Thecal spacing is 10–11 in 10 mm on mature stipes. Curved thecal form appears to be identical to that of *Tetragraptus serra*.

Genus *TETRAGRAPTUS* Salter, 1863

TYPE SPECIES. *Fucoides serra* Brongniart 1828.

CLASSIFICATION of '*Tetragraptus*'. Quadriramous dichograptoids have traditionally been placed in Salter's genus *Tetragraptus*. It has long been recognized (Nicholson & Marr 1895, Elles 1922) that such a diverse range of forms was bound to include members of different phyletic lineages. The above authors and Bulman (1955, 1963, 1970) regarded *Tetragraptus* as representing a stage or grade in the transition from multiramous to pauciramous species along a number of different lineages. They thus accepted the form genus *Tetragraptus* as a polyphyletic, but useful, grouping of species.

Attempts to subdivide the genus (Bouček & Přibyl 1951, Bouček 1973, Obut 1957, Ruedemann 1904) have generally followed the same lines as those of attempts to subdivide *Didymograptus* and they suffer from the same shortcomings. Many of our comments in discussion of the classification of *Didymograptus* apply here, particularly those relating to the use of general rhabdosome shape as the principal basis of generic classification. Features of general rhabdosome morphology, particularly the attitude or arrangement of second-order stipes, have been used as either the sole, or the main, basis for recognizing subgenera or genera within the old concept of *Tetragraptus*. The following have been proposed: *Tetragraptus* (*Etagraptus*) Ruedemann 1904, *T.* (*Eotetragraptus*) Bouček & Přibyl 1951, *Pendeograptus* Bouček & Přibyl 1951, *Paratetragraptus* Obut 1957, *Tetragraptus*, s.s. or *Tetragraptus* (*Tetragraptus*) Bouček & Přibyl 1951. The second, third and fifth of these were, in effect, merely formal upgradings of the three informal groups of tetragraptid species of Elles & Wood 1902. All five were regarded as synonyms by Bulman (1970) who maintained the broad concept of *Tetragraptus* as a form genus, but the subgenera were raised to full generic rank by Bouček (1973) who reaffirmed his faith in their phyletic integrity.

1. Subgenus *Etagraptus* Ruedemann, 1904, was based on *T. (E.) lentus* Ruedemann 1904. It was extended to include those tetragraptids with H-shaped rhabdosomes such as the important zonal species *T. approximatus*. However the type, *T. (E.) lentus*, is a distinctive form with long slender sicula and initial pair of thecae, characters which distinguish it from *T. approximatus* and its allies, but which link it with species here assigned to the Sigmagraptinae. Thecae of

second-order stipes match those of sigmagraptines and differ markedly from those of the *T. approximatus* group. *Etagraptus* is therefore here regarded as belonging to the Subfamily Sigmagraptinae and is further discussed under that heading. For the remaining species included by Ruedemann in *Etagraptus*, the name *Paratetragraptus* Obut 1957 is used.

2. Subgenus *Eotetragraptus* Bouček & Přibyl, 1951, was erected to include species with stipes developed in the horizontal plane. It originally included those with H-shaped rhabdosomes but was later (Bouček 1973) restricted to species in which the second-order stipes are disposed more or less at right angles. *T. quadribrachiatus* is the type species. However, according to its definition, the subgenus also includes such improbable companions as *T. headi*, with its long curved thecae of *T. serra* type, and *T. harti*, with slender thecae of low inclination. It seems highly improbable that these three forms are closely related. Unfortunately the development and proximal structure of *T. quadribrachiatus* are not known as the species has not yet been described from relief material. It is thus not possible to define the subgenus *Eotetragraptus* in a phyletically meaningful way and it is not used here.

3. The genus *Pendeograptus* Bouček & Přibyl, 1951, was erected for tetragraptids with pendent rhabdosomes and was based on *T. pendens* Elles 1898. It includes *T. fruticosus* and a number of forms close to *T. fruticosus* or *T. pendens* figured by Ruedemann (1947: pl. 51); also such forms as *T. cf. pendens* of Cooper (1979: fig. 34a; pl. 6c). Some details of the proximal region of *T. fruticosus* (*s.l.*) are known from material we describe herein. The sicula is long and wedge-shaped, and th1¹ relatively straight; the whole aspect of the proximal region resembles that of a bryograptid rather than of a dichograptid. Development is of isograptid type. Thecae of second-order stipes have acute, projecting, denticulate apertural margins and deeply recessed apertural 'excavations', again more like thecae of a dendroid than of a graptoloid. Once again, however, details of the proximal region of the type species, *T. pendens*, are unknown and the species has not yet been described from relief material. For this reason, inclusion of *T. fruticosus* within the genus, and the validity of the genus itself, is provisional. Specimens figured as *T. pendens* from Victoria by Thomas (1960: pl. 3, fig. 31), from New Zealand by Cooper (1979: fig. 34a; pl. 6c) and from North America by Ruedemann (1947: pl. 51, figs 18–25) suggest that there is an array of forms lying between *T. fruticosus* and the typical *T. pendens* of Elles, supporting the inclusion of both within the one genus. We therefore tentatively accept *Pendeograptus* as a subgenus of *Tetragraptus*, redefined on proximal characters.

4. The genus *Paratetragraptus* Obut, 1957, was erected for *T. approximatus* and its allies with H-shaped rhabdosomes, but excluding *T. lentus* Ruedemann, 1904, which is not closely related to *T. approximatus*. The group so defined would include *T. acclinans* Keble, *T. vestrogothus* Törnquist and the various forms from North America figured by Ruedemann (1947: pl. 52, figs 4–27), and does appear to be reasonably distinct and definable on its rhabdosome shape. Included forms are all of similar age (basal Arenig), have generally similar thecal characteristics, and might well constitute a monophyletic group.

Sicular morphology and proximal structure are not known in *T. approximatus*, or for that matter in any other member of the group, and its recognition as a valid subgenus remains unsupported by data on proximal morphology. Our acceptance of *Paratetragraptus* as a subgenus is therefore provisional. In life, the stipes presumably lay in a horizontal plane with respect to the sicula, since the sicula is almost invariably not seen in profile view.

5. *Tetragraptus*, *sensu stricto* as used by Bouček (1973) includes groups IV (*T. serra*) and V (*T. bigsbyi*) of Elles & Wood 1902. Bouček's diagnosis is as follows:

'Rhabdosome pendent [sic], sicula well developed, free. Stipes more or less parallel to sicula; at least one stipe of each pair of stipes in a reclined up to scandent position. When preserved in horizontal plane, thecae of one pair of stipes are on the inner side, those of the other pair on the external side of the stipes'. Type species is *Fucoides serra* Brongniart 1828. From the diagnosis the group is defined principally on the possession of strongly reclined (assuming that the word 'pendent' in the diagnosis is a misprint) or scandent stipes. From his list of included species (Bouček 1973: 20 – *T. amii* Elles & Wood, *T. bigsbyi* (Hall),

T. erectus Mu, Ge & Yin, *T. kindlei* Ruedemann, *T. phyllograptoides* Linnarsson, *T. pseudo-bigsbyi* Skevington, *T. taraxacum* Ruedemann and *T. woodae* Ruedemann) all degrees of reclination, from weakly reclined (*T. amii*) to highly inclined (*T. bigsbyi*), are included, although the former would appear to be excluded by the diagnosis.

The group contains the type species of the genus *Tetragraptus* Salter, 1863, *T. serra*, some proximal details of which are interpreted herein from isolated growth stages from Spitsbergen. The sicula is very long and massive, the first theca arising near the apex of the sicula on its ventral (virgellar) side. The growth and development, as far as can be traced, is similar to that in the better known *T. bigsbyi* (Bulman 1970: fig. 53), *T. reclinatus reclinatus*, *T. r. toernquisti* and *T. phyllograptoides*, the last three of which are described herein. The differences between them are slight to moderate differences of size and tenuity of the sicula and proximal thecae and we would not rank them as important differences in structure.

There is thus a group of species with proximal features similar to those of *T. serra* and, by definition, this group should be regarded as *Tetragraptus*, s.s. The concept of *Tetragraptus*, s.s., as the nominate subgenus, is thus retained but is here based on proximal features as well as, rather than solely on, stipe attitude.

For the majority of species at present referred to the form-genus *Tetragraptus*, and in which proximal morphology is unknown, the general (form-genus) concept of *Tetragraptus* must be retained. As with the didymograptids it may be some time before we can switch over to a wholly phylogenetically based classification. The form-genus *Tetragraptus*, s.l., is here used to include the majority of (poorly known) species together with the three phyletically-based subgenera. We stress that we do not imply the subgenera are phyletically related within the old form-genus. It is much more likely that *Pendeograptus* and *Paratetragraptus* are more closely related to species and genera outside *Tetragraptus*, s.l., than to those within it, and that they will eventually be raised to full generic rank. The system has the advantage of retaining a measure of nomenclatorial stability, especially for important zonal species such as *T. (Paratetragraptus) approximatus* and *T. (Pendeograptus) fruticosus* while yet using a grouping that reflects inferred phyletic relationships. It should be recognized that, as with *Didymograptus*, the proposed classification is in concept a dual one.

Form-genus **TETRAGRAPTUS** Salter, 1863 (= *Tetragraptus*, s.l.)

Subgenus **TETRAGRAPTUS** Salter, 1863

TYPE SPECIES. *Fucoides serra* Brongniart 1828.

DIAGNOSIS. Sicula long and broad, th1¹ arising near apex and diverging sharply from near base. Thecae 1² and 2¹ grow out horizontally, their proximal portions together forming a massive structure representing the two 'crossing canals'. Development of isograptid type, dextral or, rarely, sinistral. Dicalycal th3¹ (right-handed) and th3² (left-handed), all development on the reverse side. Two orders of progressive dichotomy. Second-order stipes reclined to scandent, thecae curved with high distal inclination.

SPECIES: *Fucoides serra* Brongniart 1828, *Graptolithus bigsbyi* Hall 1865, *Tetragraptus phyllograptoides* phyllograptoides Strandmark 1902, *T. p. triumphans* Cooper & Fortey subsp. nov., *T. reclinatus* Elles & Wood 1902, and *T. r. toernquisti* Monsen 1937.

The following species are provisionally included: *Tetragraptus amii* Elles & Wood 1902, *T. bigsbyi* var. *divergens* Monsen 1937, var. *askerensis* Monsen 1937, and var. *ascendens* Monsen 1937, *T. reclinatus abbreviatus* Bouček 1956, *T. pseudobigsbyi* Skevington 1965, *T. rigidus* Ge 1964, *T. hsui* Ge 1964, and *T. isograptoides* Ge 1964.

The following are doubtfully included: *Tetragraptus mobergi* Monsen 1937, *T. woodae* Ruedemann 1904, *T. minutus* Ge 1964, and *T. ovalis* Ge 1964.

DISCUSSION. The proximal morphology and development are known in detail in several species. The sicula is relatively massive and the first theca diverges from it at a sharp angle. Thecae 1² and 2¹ diverge from each other in the horizontal plane and their proximal portions together form a massive bulge on the reverse side of the sicula and th1¹. The initial portion of

th¹² is dorsoventrally wide, equivalent to about $\frac{1}{3}$ the length of the sicula. The second-order stipes are produced from dicalyca thecae 3¹ (which is right-handed) and 3² (left-handed), the branching type on both sides being isograptid. All development thus takes place on the reverse side of the rhabdosome. The reclined growth of second-order stipes commences from their first theca in *T. (T.) serra* and *T. (T.) phyllograptoides triumphans*, but is more gradually introduced in *T. (T.) reclinatus reclinatus* and *T. (T.) r. toernquisti*.

The species provisionally included above are known only from flattened material. Details of their proximal morphology are not known but they have a general resemblance in rhabdosome form. Those doubtfully included are too poorly known or described to allow a reasonably confident assignment. It is highly probable that several of the above-listed names are synonyms.

Tetragraptus (Tetragraptus) serra serra (Brongniart 1828)

Figs 14a–e, 15a–e, 16, 17, 18; Pl. 3, fig. 5

- 1828 *Fucoides serra* Brongniart: 71; pl. VI, figs 7, 8.
 1858 *Graptolithus bryonoides* J. Hall: 126.
 1865 *Graptolithus bryonoides* J. Hall; Hall (*pars*): 84; pl. III, figs ?11, ?12; pl. IV, figs 1, 4, 6–8, ?11; non pl. IV, figs 9, 10 (= *T. amii* Elles & Wood); non pl. IV, figs 2, 3 (= *T. reclinatus toernquisti* Monsen).
 1875 *Tetragraptus bryonoides* (Hall) Nicholson: pl. VII, figs 4, 5.
 1877 *Graptolites (Didymograpsus) bryonoides* (Hall) M'Coy: 16–17; pl. 2, figs 2, 3, ?5.
 1902 *Tetragraptus serra* (Brongniart) Elles & Wood (*pars*): 65–67; pl. VI, figs 4a–c, f only.
 1904 *Tetragraptus serra* (Brongniart); Ruedemann (*pars*): 655–657, text-figs 56, 57; pl. 11, figs 8–10 only.
 1904 *Tetragraptus serra* (Brongniart); Törnquist: 8–10; pl. 1, figs 17–21.
 1937 *Tetragraptus serra* (Brongniart); Monsen: 169; pl. 4, figs 13, 18, ?22, ?28; pl. 12, figs 2, 3; pl. 19, fig. 10.
 1960 *Tetragraptus serra* (Brongniart); Thomas: figs 28–30.
 1960 *Tetragraptus serra* (Brongniart); Berry: 56; pl. 6, fig. 6; pl. 13, fig. 1.
 1963 *Tetragraptus serra* (Brongniart); Ross & Berry: 79–80; pl. 3, fig. 6.
 1979 *Tetragraptus serra* (Brongniart); Cooper: 66; pl. 8i; fig. 36a.

Type material

LECTOTYPE. BM(NH) 26995, herein selected; paralectotypes, BM(NH) Q5060–2. All specimens lie in the one bedding plane on a small slab of dark grey shale, and are housed in the British Museum (Natural History). There are no other recognizable species in the slab.

The original specimens of Brongniart's *Fucoides serra*, like those of his *Fucoides dentatus* (Bulman 1963), have long been believed lost and the identity of the form *serra* has been the subject of much confusion, particularly in relation to *Tetragraptus amii* Elles & Wood and *Graptolithus [Tetragraptus] bryonoides* J. Hall.

The original slab was collected from Point Levis by 'M. Stokes' (probably Charles Stokes), and acquired by Dr Bigsby who eventually presented it to the British Museum as part of a larger collection of Levis material; it has remained unrecognized as such until the present. From Brongniart's somewhat diagrammatic figures, particularly that showing the whole slab with five fragmentary rhabdosomes (1828: pl. VI, fig. 7), there can be no doubt that slab now in the BM(NH) is that used by Brongniart in erecting the species. The uppermost rhabdosome in his fig. 7 is that refigured here as Fig. 14e and the lower group of rhabdosomes are refigured here in Fig. 14a–d. The specimen of Fig. 14e, which is here chosen as **lectotype**, is the most complete and also most clearly shows the reclined attitude of the stipes.

STRATIGRAPHIC HORIZON. The horizon from which the lectotype comes is, unfortunately, unknown. '*T. serra*' is listed from Zones A, C1, D1 and D2 by Raymond (1914).

DESCRIPTION of type series. Details of sicula and proximal development and structure are not visible. Primary stipes apparently composed of one theca each. Second-order stipes up to 24 mm long, moderately reclined, with gentle, dorsally concave curvature following their

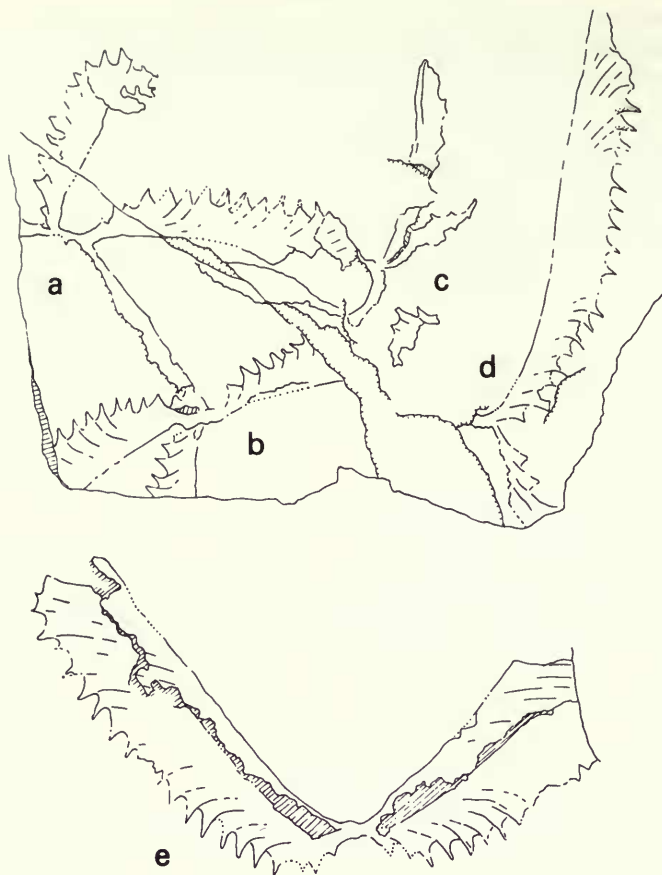


Fig. 14 *Tetragraptus (Tetragraptus) serra serra* (Brongniart), type specimens. a–d, paratypes, preserved near edge of slab, the outline of which is shown: a, BM(NH) Q5060; b, Q5061; c, fragmentary specimen; d, Q5062. e, **lectotype**, BM(NH) 26995, in same slab as paratypes. All $\times 2.5$.

initial sharper curvature, becoming straight distally. Stipe width at the level of any given thecal aperture varies from specimen to specimen (Fig. 15); maximum stipe width ranges from about 3.7 mm (Q5062) to 4.2 mm in the lectotype (26995). Some of this variation is probably the result of the preservation process (see below) but some is likely to reflect variation in the original rhabdosomes. It is not possible to determine the relative proportions of each except to note that in Q5062, with relatively narrow stipes, the apertural margins show deep 'excavations' and thecal inclination is not noticeably reduced. This suggests that the stipe was orientated with its sagittal plane more or less parallel with the plane of bedding prior to burial and not rotated to present a partially dorsal view. Thus its narrow stipes are a primary feature and the range of the population in original dorsoventral stipe width is likely to have been considerable.

Thecae are strongly curved, particularly near their apertures where their angle of inclination exceeds 90° . Ventral apertural margins project prominently and lateral apertural margins are deeply recessed, producing deep 'excavations'. They are spaced 8.5 in 10 mm in the lectotype, and 8.6 to 9.5 in 10 mm in the paralectotypes.

DISCUSSION of type series. The lectotype and paralectotypes together show well the variation that can be introduced by distortion of the rhabdosome prior to and during burial. Because of the attitude of its stipes it is inevitable that, when the rhabdosome is preserved in a flat plane, as

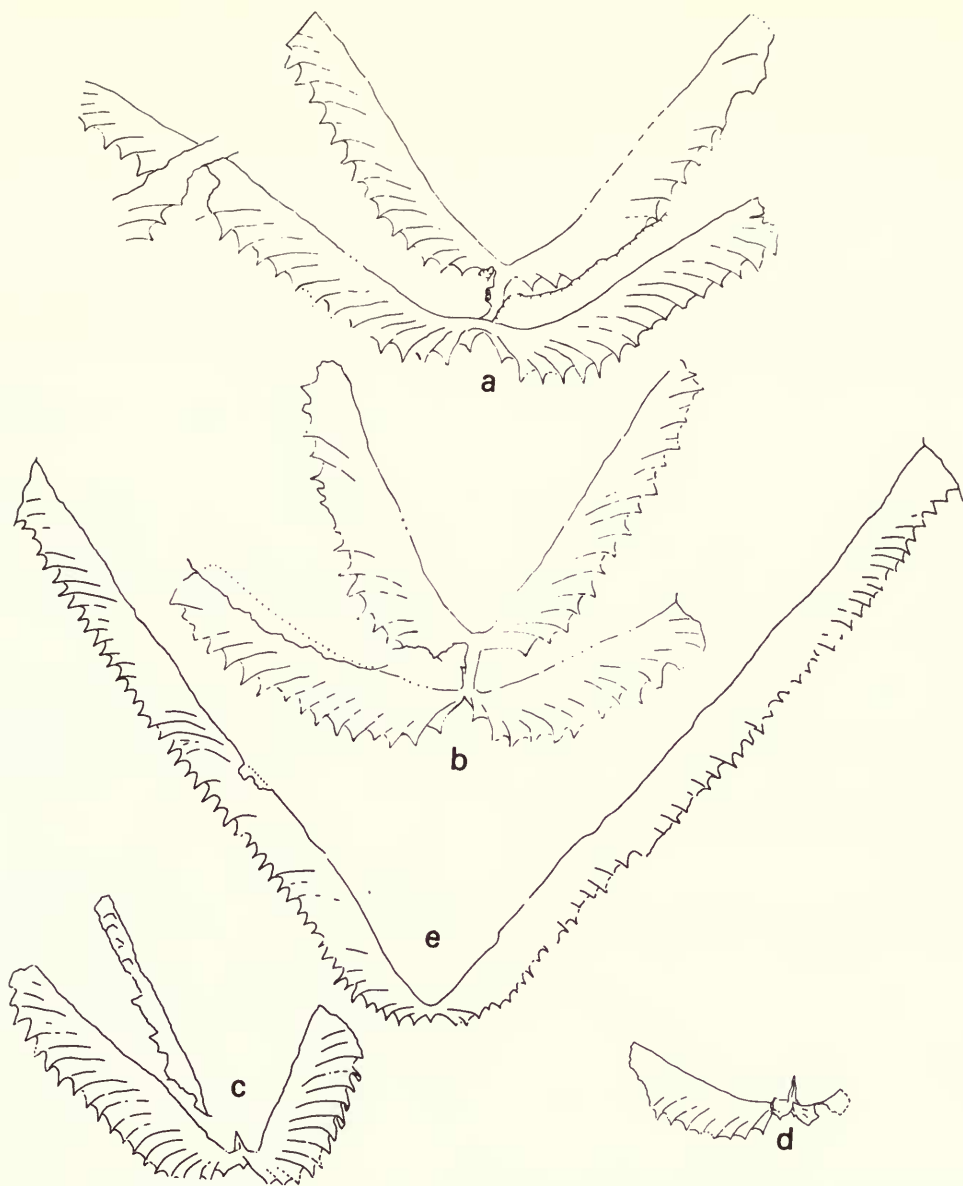


Fig. 15a–d *Tetragraptus* (*Tetragraptus*) *serra serra* (Brongniart) from Spitsbergen. a, SM A105789, mature rhabdosome preserved in relief in limestone, 15–24 m above base of Olenidsletta Member, southern section; $\times 3$. b, A105743, lower part of Olenidsletta Member on Olenidsletta (see Pl. 3, fig. 5); $\times 3$. c, PMO NF2788, 23 m above base of Olenidsletta Member, southern section; $\times 2.5$; d, A105792, in partial relief, 15–24 m above base of Olenidsletta Member, $\times 2.5$.

Fig. 15e *Tetragraptus* (*Tetragraptus*) *serra* subsp. 1. A105801, 9.5–15 m above base of Olenidsletta Member, southern section; $\times 1.7$.

is usual in shale, it will suffer distortion and rotation of the stipes. If it is preserved 'on its side', with either the median plane or bilateral plane of the rhabdosome parallel to the bedding, the upper pair of stipes fold down upon the lower pair of stipes, both pairs retaining their reclined attitude, as in Fig. 14e. On the other hand, if it is preserved on its base (or inverted, on the tips of its stipes) then the stipes will be splayed out and one or more will usually be bent or rotated.

There are all intermediates between the two end modes, and a great range in the final attitude of the stipes results. Also, measurements of stipe width are likely to be decreased by torsion along the stipe or twisting, so that it is not seen in full profile view, particularly in rhabdosomes preserved in the second mode above.

These factors undoubtedly contribute to the variation shown by the type series, and in populations from Spitsbergen and elsewhere. There is little doubt that the lectotype and paralectotypes all represent the one species, despite their wide range of variation in stipe attitude and width. Some of the variation no doubt reflects morphological variation of the original rhabdosomes but some, particularly that in stipe attitude, results from the vagaries of preservation. For these reasons there seems little point in attempting to distinguish species in flattened material on subtle differences in stipe attitude and width.

RELATIONSHIPS with *Graptolithus bryonoides* J. Hall and *Tetragraptus amii* Elles & Wood. The name *Graptolithus bryonoides* was introduced by Hall in 1858 but was accompanied neither by figures nor by specification of specimens studied by him. His fuller description and figures of 1865 can be regarded as a subsequent validation and the figured specimens as syntypes. Nine specimens were figured, of which two (those of his pl. 3, figs 11, 12, and pl. 4, fig. 4) were only questionably included in the species. In a footnote Hall (1865: 84) states 'I have little doubt that this species is identical with *Fucoides serra* of Brongniart . . .', of which he had only recently become aware, and 'the figures of Brongniart correspond with figs 9 and 10 of plate 4 of this memoir'. Although in the figure caption of these two specimens Hall had added the proviso that 'Figs 9 and 10 may possibly prove to be a distinct species' he nevertheless clearly regarded the name *bryonoides* as being a junior synonym of *Fucoides serra*.

Most subsequent authors, however, have considered Hall's *bryonoides* to comprise two forms, one 'in which the stipes are spread out in what may be termed a "*quadribrachiatus*" fashion' (i.e. more or less horizontal), represented by his figs 9 and 10, and one 'in which the stipes are directed obliquely upward' (reclined) represented by pl. 4, figs 1–8, 11 (Elles & Wood 1902: 66). Opinions as to which of the two forms the name *serra* should apply have differed, unfortunately, leading to much confusion in meaning of the name *serra*. Whereas Elles & Wood regarded the reclined form as *serra* and the 'horizontal' form as identical with Lapworth's (MS) species *Tetragraptus amii*, Törnquist (1904) took the opposite view and regarded the 'horizontal' form as *serra* and, although he did not state so specifically, the reclined form as *bryonoides*. Some subsequent Swedish and most Australasian workers have followed Törnquist, using the names *serra* and *bryonoides* whereas most British and North American workers have followed Elles & Wood and used the names *amii* and *serra* respectively for the same two species. The latter usage has clearly gained the widest acceptance.

The problem can only be resolved by the designation of lectotypes and redefinition of the species. Rediscovery of the type specimens of Brongniart's *Fucoides serra* in the British Museum (Natural History) now enables us to do this and lectotypes for all three species are therefore proposed herein. It is necessary, however, to introduce a further complication. Among the specimens generally attributed to *T. serra*, *sensu* Elles & Wood, are two (Hall's 1865: pl. 4, figs 2, 3) which differ in having stipes which are narrow and declined rather than reclined and thecae with a lower angle of inclination. It would seem that the two specimens are unlikely to represent the same species as that represented by the others and they are here excluded and referred to *T. reclinatus toernquisti* Monsen.

LECTOTYPE for *Graptolithus bryonoides* Hall 1858. Various courses are open in the selection of a lectotype for *G. bryonoides*. The one which seems to be consistent with the most widely accepted usage is to select a specimen from the group referred to *serra* by Elles & Wood (excluding the specimens of pl. 4, figs 2 and 3), thus making *bryonoides* a junior synonym of *serra*, and to retain *amii*, based on British material, as a distinct species. Specimen GSC 978, held in the Geological Survey of Canada, Ottawa, and figured by Hall (1865) as pl. 4, figs 1 and 6, is therefore here designated **lectotype** and refigured (Fig. 16). Paralectotypes: GSC 922b, figured by Hall (1865: pl. 4, fig. 4); GSC 922a (Hall 1865: pl. 4, figs 7, 8); ?GSC 922g (Hall 1865: pl. 6, fig. 4), very poorly preserved. The originals of Hall's 1865: pl. 3, figs 11, 12, are

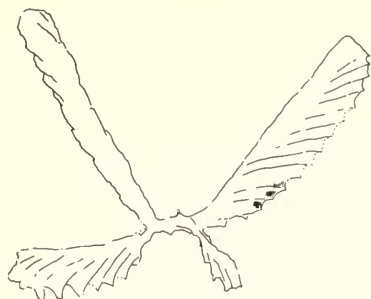


Fig. 16 *Tetragraptus (Tetragraptus) serra serra* (Brongniart). **Lectotype** of *Graptolithus bryonoides* Hall, GSC 978. Specimen figured by Hall (1865: pl. 4, figs 1, 6). $\times 2.5$.

indeterminate stipe fragments and those of his pl. 4, figs 5, 11, although not seen by us, appear to be similarly incomplete and indeterminate. The originals of Hall's 1865: pl. 4, figs 9, 10 (not seen by us) are regarded as belonging to *Tetragraptus amii* Elles & Wood, and those of his pl. 4, figs 2, 3 as belonging to *Tetragraptus reclinator toernquisti* Monsen.

Thus defined, *G. bryonoides* clearly belongs to Brongniart's species *Fucoides serra*. Stipe attitude, curvature and width, thecal spacing and outline match well. Maximum stipe length is 42 mm, longer than that of the types but unlikely to be of diagnostic value.

Ge (1964) separated the specimens of Hall's pl. 4, figs 4, 7, 8 and 11 and referred them to his new species *T. rigidus*, but there seems little justification in discriminating between these and that of Hall's fig. 2; they merely represent more advanced growth stages. *T. rigidus* from the Ningkuo Shales of late Arenig to Llanvirn age is distinguished from *bryonoides* (and *serra*) by its more robust rhabdosome and rigid, highly reclined stipes. It is probably the best name for the forms listed as *T. cf. serra* from the late Castlemainian and Yapeenian of New Zealand by Cooper (1979: 67; pl. 8, figs g, k).

Spitsbergen material

STRATIGRAPHIC RANGE. Olenidsletta Member, V₁b, 9–25 m above base; early Arenig.

MATERIAL. SM A105789–93, PMO NF2787–8.

DESCRIPTION. Sicula 2.3 mm long (measured in specimen SM A105792). The first-order stipes are comprised of a single theca each. Second-order stipes increase rapidly in width, reaching a maximum of 3.0–4.0 mm by the level of the 5th to 8th theca (Fig. 17). Stipes are moderately reclined and initially curved but become straight distally, as in the type material. Maximum length 30 mm, but longer isolated stipe fragments may belong to the species.

Thecae in the mature part of the stipe are inclined initially at about 30°–35°; distally they are inclined to about 95° but the free ventral wall often appears to be flexed downwards apparently from deformation during burial (Fig. 15). Apertural margins are deeply recessed leaving a protruding ventral process, but again the outline of the apertural margin varies widely with mode of preservation. Thecae are spaced 9.5–11.5 in 10 mm in the proximal part of the stipe, and 9.0–10.0 in 10 mm in the distal part.

DEVELOPMENT. Several growth stages have been isolated by acid treatment, of which two are figured (Fig. 18a, b). Although most have been flattened or otherwise distorted, they enable several details of development to be determined. Theca 1¹ originates high on the sicula, probably on the prosicula although this structure is not clearly defined. Theca 1¹ grows down the ventral side of the sicula and turns sharply out near the sicular aperture, as in *T. bigsbyi* (Bulman 1970: fig. 53). Theca 1² originates from 1¹ at a point level with the mid-length of the sicula. It immediately expands and gives rise to th2¹. The proximal portion of the th1² and 2¹ together comprise a massive structure, containing the 'crossing canals', on the reverse side of the rhabdosome. The whole aspect of the proximal region is more robust than in *T. bigsbyi*. Development is isograptid and dextral and conforms closely to that of *T. bigsbyi*. Details of second-order branching are unknown.

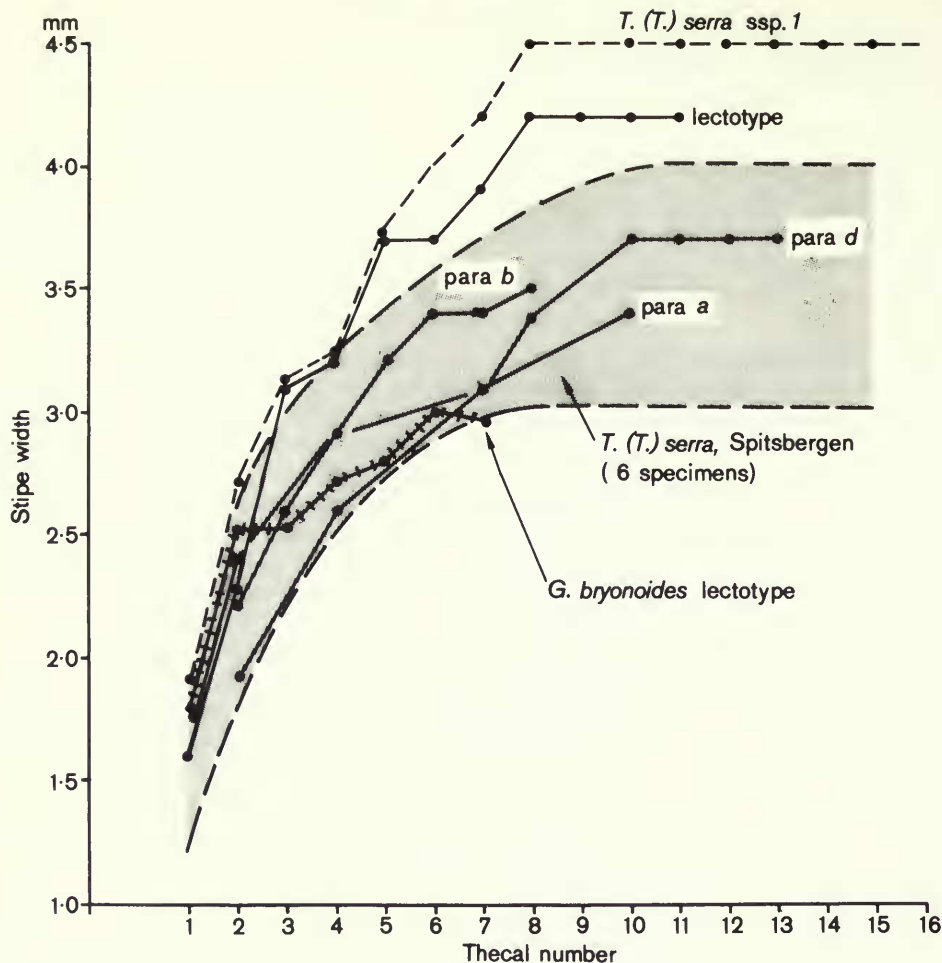


Fig. 17 Stipe expansion diagram, *Tetraraptus* (*Tetraraptus*) *serra serra* (Brongniart), type series, and the lectotype of *Graptolithus bryonoides* Hall (= *T. (T.) serra serra*). The field for 6 specimens from Spitsbergen is stippled. Expansion curve for *T. (T.) serra* subsp. 1 is also shown.

DISCUSSION. The proximal structure of *T. serra*, as described here, not unexpectedly matches closely that of *T. bigsbyi* described by Bulman (1970: fig. 53). It differs from those growth stages assigned to *T. cf. serra* by Skevington (1965: figs 11–13) in the lower point of origin of $th1^2$.

The Spitsbergen material indicates a considerable range of variation in maximum stipe width, no doubt in part the result of preservation. It differs from the type material only in having fractionally narrower thecal spacing.

The comparatively wide range of stipe width here described for *T. serra* calls into question the distinctness of such species as *T. pseudobigsbyi* Skevington 1965 which are of *serra* type and whose maximum stipe width (2.9–3.2 mm) lies within the *serra* range. Several somewhat slender but poorly preserved forms are present in the Spitsbergen populations of *T. serra*. However, because of its closer thecal spacing (12–13 in 10 mm) *T. pseudobigsbyi* is retained as a distinct species. It should be noted that Skevington's figured specimens of both *T. pseudobigsbyi* and *T. bigsbyi* present an a, b stipe pair, rather than the more familiar orientation of a 1, 2 stipe pair with the sicula between them.

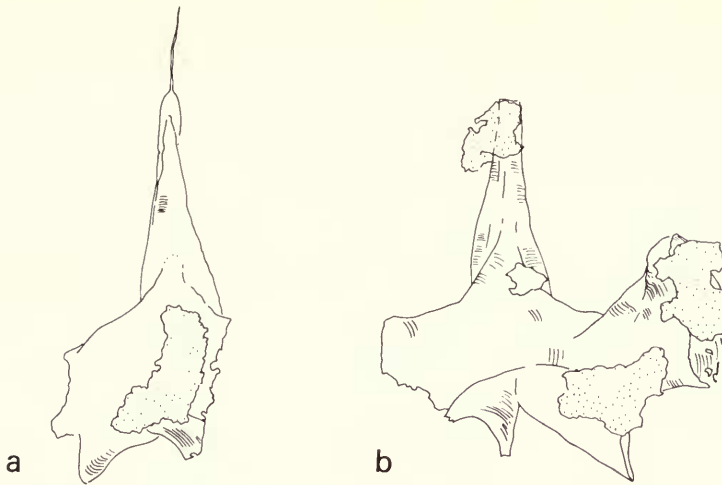


Fig. 18 *Tetragraptus* (*Tetragraptus*) *serra serra* (Brongniart), growth stages. a, SM A105795, fragmentary stage showing high origin of th1' and proximal portions of th1² and th2'. b, A105796, incomplete later stage showing apertural region of th1', proximal part of th2' and partly formed th3'. Both from 16–17 m above base of Olenidsletta Member, $\times 20$.

None of the specimens figured by Ruedemann (1947: pl. 50, figs 19–23) under the name *T. serra* appear to belong to Brongniart's species, but two (those of his figs 22, 23) are referred to *T. serra* subsp. 1 below.

T. rigidus Ge (1964) from the Ningkuo Shale of China differs from *T. serra* only in its more rigidly reclined stipes and slightly more widely spaced thecae and is probably best regarded as a stratigraphically younger subspecies.

***Tetragraptus serra* subsp. 1**

Fig. 15e; Pl. 5, fig. 8

1902 *Tetragraptus serra* (Brongniart) Elles & Wood (*pars*): pl. 6, fig. 4d only.

1947 *Tetragraptus serra* (Brongniart); Ruedemann (*pars*): pl. 50, figs 22, 23, *non* figs 19, 20.

STRATIGRAPHIC RANGE. Olenidsletta Member, V₁b, 8–19 m, above base.

MATERIAL. SM A105797, SM A105801, and several other incomplete specimens.

DESCRIPTION. The form differs from *Tetragraptus serra serra* mainly in its more robust rhabdosome. Details of development and proximal structure are unknown but the general aspect of the proximal region is like that of *T. serra serra*. Second-order stipes are more sharply flexed and more highly reclined and commonly have gentle (dorsally) convex curvature for the first 20 mm of their length. They widen at the same rate but reach a greater maximum width (4.4–4.7 mm, Fig. 17). Thecal spacing (9 in 10 mm) and curvature match those of *T. serra serra*.

DISCUSSION. The specimens are here separated from *T. serra* because they appear to lie just outside its field of variation. In view of the wide range of variation in stipe width described here in *T. serra*, however, it is possible that the full range of the species, when it is better known, will be found to include such forms; they are therefore here left in open nomenclature.

The specimens figured by Ruedemann (1947: pl. 50, figs 22, 23) from Idaho (zone not given) as *T. serra* match this Spitsbergen form well. *T. rigidus* Ge (1964) is a similarly rigid form but has more strongly reclined stipes and slightly more widely spaced thecae.

Tetragraptus (Tetragraptus) amii Elles & Wood 1902

Fig. 19a–f; Pl. 5, figs 6, 9

- 1865 *Graptolithus bryonoides* J. Hall; Hall (*pars*): 84; pl. 4, figs 9, 10; *non* pl. 3, figs 11, 12; pl. 4, figs 1, 4, 6–8, ?11 (= *T. serra* Brongniart); *non* pl. 4, figs 2, 3 (= *T. toernquisti* Monsen).
 1902 *Tetragraptus amii* Elles & Wood: 60–62; pl. 5, figs 4a–c (*ex* Lapworth MS).
 1904 *Tetragraptus serra* (Brongniart); Törnquist: 8–10; pl. 1, figs 17–21.
 1947 *Tetragraptus amii* Elles & Wood; Ruedemann: 301–302; pl. 50, figs 12–14.
 1960 *Tetragraptus amii* Elles & Wood; Berry: 52; pl. 6, fig. 10; pl. 7, fig. 9.
 1963 *Tetragraptus amii* Elles & Wood; Ross & Berry: 74–75; pl. 3, fig. 1.
 1979 *Tetragraptus amii* Elles & Wood; Cooper: 60; pl. 7, fig. g.

LECTOTYPE. SM A17838, figured by Elles & Wood (1902: pl. 5, fig. 4b) and held in the Sedgwick Museum, Cambridge, is here designated **lectotype**.

STRATIGRAPHIC LEVEL. Olenidsletta Member, 49–87 m above base, V_1c – V_2a .

MATERIAL. PMO NF2817, NF3321–5.

DESCRIPTION. Sacula is 1.7 mm long but is seldom visible. First-order stipes are comprised of one theca each. Second-order stipes reach up to at least 23 mm long. They widen rapidly, as in *Tetragraptus serra*, reaching nearly their maximum width of 2.4 to 2.7 mm by the level of the 3rd or 4th theca. They are straight or have slight, dorsally concave, curvature. Divergence angle is highly variable in the flattened specimens from reclined to 'horizontal'. Rhabdosomes are very robust and the stipes often appear to have been buckled and rotated somewhat during preservation. Their original attitude is thought to have been gently reclined so that on flattening they generally splay out in a *quadribrachiatus*-like fashion (Fig. 19a). Immature rhabdosomes with short second-order stipes are often preserved with 'reclined' stipes (Fig. 19c).

Thecae are relatively straight and inclined at about 45° near their apertures. Apertural margins are deeply indented, giving a distinctively deeply serrated ventral margin to the stipe. They are spaced 11–13 in 10 mm in the proximal part of the stipe and 9–10 in 10 mm in the distal part.

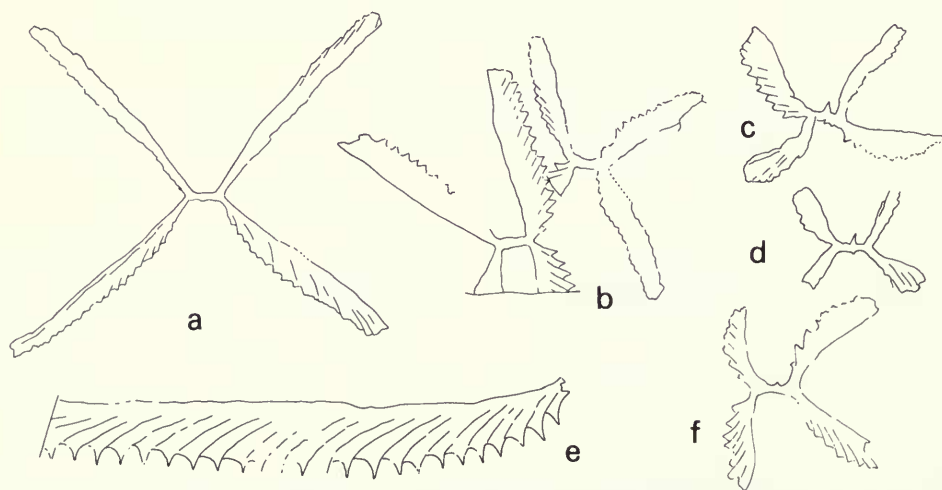


Fig. 19 *Tetragraptus (Tetragraptus) amii* Elles & Wood. a, PMO NF3324, complete mature specimen, in black shale band 49 m above base of Olenidsletta Member, southern section; $\times 2$. b, two superimposed rhabdosomes, NF3323 below and NF3322 above, same horizon as a, $\times 2$. c, NF3321, immature form, same horizon as a, $\times 2$. d, NF3325, immature form, same horizon as a, $\times 2$. e, NF2817, incomplete mature stipe preserved in full relief in limestone, 87 m above base of Olenidsletta Member, $\times 3$. f, SM A109734, immature form attributable to either *T. (T.) amii* or *T. (T.) serra serra*, 40–43 m above base of Olenidsletta Member, type section; $\times 2.5$.

DISCUSSION. Although Elles & Wood (1902) state that a maximum stipe width of 3.0 mm is most commonly met with, their figures (pl. 5, figs 4a–c) show that forms with more slender stipes (2.4–2.7 mm) were present, and it is with these more slender forms that the Spitsbergen material may be compared.

The distinction of *T. amii* from *T. serra serra* depends largely on its straighter and less strongly reclined stipes, and, less reliably, on its somewhat more slender stipes. When we can estimate the full range of variation of *T. amii* more reliably, it may be found to intergrade with that of *T. serra serra*, in which case its status as a distinct species would have to be reviewed.

Tetraraptus (Tetraraptus) bigsbyi (Hall 1865)

1865 *Graptolithus bigsbyi* J. Hall (*pars*): 86–88; pl. 16, figs 25–26, 29, 30.

1964 *Tetraraptus hemirotundus* Ge: 384–385, 399; pl. 3, figs 7–13.

1965 *Tetraraptus bigsbyi* (Hall) Skevington: 4–8, figs 1, 3, 5, 6.

1979 *Tetraraptus bigsbyi* (Hall); Cooper: 62; pl. 8b, e; fig. 30.

STRATIGRAPHIC RANGE. 29–31 m above base of Olenidsletta Member, V₁b, early Arenig.

MATERIAL. SM A105798. Sedgwick Museum, Cambridge.

DESCRIPTION AND DISCUSSION. Although poorly preserved, the Spitsbergen specimen shows the characteristic small ovate rhabdosome outline with convergent second-order stipes of *T. bigsbyi*. The rhabdosome is 13 mm in length and 10 mm in width. Details of proximal development and structure are unknown. Second-order stipes are about 3.5 mm in maximum width which lies near the midpoint along their length. Thecae are spaced about 12 in 10 mm (6 in 5 mm).

The forms described as *T. hemirotundus* sp. nov. by Ge (1964: 399; pl. 3, figs 7–13) differ from *T. bigsbyi* only in having short (up to 6.5 mm long) second-order stipes. They may merely represent incompletely grown rhabdosomes. If the stated scale of the figured specimens is correct, then stipe width is nearer to 2.5–3 mm than to the 4 mm stated in the text. Ge's figured specimens best match those assigned to *T. bigsbyi* by Cooper (1979: 62; pl. 8b, e; fig. 30) which differ from Skevington's lectotype in their narrower (and shorter) second-order stipes. Since maximum stipe width is reached only near the midpoint of the stipes (at the 9th theca in the lectotype) incompletely grown rhabdosomes with shorter second-order stipes, such as those of China and New Zealand, are likely to attain a somewhat smaller maximum stipe width than that attained by mature rhabdosomes. For this reason, the Chinese and New Zealand forms are here included in the species.

Tetraraptus (Tetraraptus) cf. isograptoides Ge 1964

Fig. 20; Pl. 4, fig. 5

cf. 1964 *Tetraraptus isograptoides* Ge: 386–387, 400; pl. 3, figs 5–6; text-fig. 6.

STRATIGRAPHIC RANGE. 145 m (topmost Olenidsletta Member, V₃b) to top of Profilbekken Member (V₄a).

MATERIAL. PMO NF1810, NF1980, NF3252, NF3315.

DESCRIPTION AND DISCUSSION. In the uppermost part of the Olenidsletta Member (V₃b) and Profilbekken Member (V₄a) are several reclined tetraraptids, most of which are preserved in relief in limestone. No specimens are sufficiently complete to give a clear idea of



Fig. 20 *Tetraraptus (Tetraraptus) cf. isograptoides* Ge. PMO NF3315, showing a 1, 2 stipe pair. From Profilbekken Member, near V₄a/b boundary; $\times 4$.

rhabdosome morphology and the following description is based on a number of incomplete specimens.

The rhabdosome is of *T. serra* type with gently to strongly reclined stipes. The sicula is about 2 mm or slightly more in length. Details of proximal development and structure are unknown. The second-order stipes are gently curved in the proximal region but become straight distally. They expand in width extremely rapidly, reaching almost their full width of 2.6–2.9 mm by the level of the second theca. Thecae are strongly curved as in *T. serra* and are spaced about 13–14.5 in 10 mm in the proximal region (measured over a stipe length of 6 to 7 mm).

The distinctive feature of the form is the rapid widening of second-order stipes, a feature which serves to distinguish the Spitsbergen material from most, otherwise similar, reclined tetragraptids, particularly *T. pseudobigsbyi*. The closest match for the Spitsbergen forms appears to be *T. isograptoides* Ge (1964: 400) described from the Ningkuo Shale of Zhejiang. From his description, Ge's species differs in its somewhat less closely spaced thecae (10 in 10 mm) and its short second-order stipes. However, because of the shortness of these stipes, estimates of thecal spacing (in 10 mm) can be derived only by extrapolating from the count in 3 or 4 mm of stipe length and are unlikely to be reliable. The short second-order stipes in the Chinese material (up to 5 mm long) more probably indicate the level of astogenetic development than constitute a reliable taxonomic character. Full sicula length (2.2 mm) in the Spitsbergen material is somewhat less than the 2.8 mm given by Ge for the Chinese material. But from Ge's figures, especially his text-fig. 6, the main difference in the Chinese form appears to be its more 'filled-in' proximal region giving it an unmistakable resemblance, as noted by Ge, to *Isograptus*.

Tetragraptus (Tetragraptus) phyllograptoides triumphans subsp. nov.

Figs 21, 22a–g; Pl. 4, fig. 3

STRATIGRAPHIC RANGE. 74.7–100.8 m above base of Olenidsletta Member, V_1c – V_3 .

MATERIAL. **Holotype**, PMO NF771; paratypes PMO NF585, NF711, NF751(a + b), NF754, NF3182; isolated specimens NF3178–81.

NAME. 'Victorious', referring to the V-shaped rhabdosome.

DESCRIPTION. The sicula is 2.3 mm long; the supradorsal portion of the sicula and first theca form a prominent 'wedge', 1.3 mm high. The first-order stipes are short and formed of a single theca each. The second-order stipes are sharply flexed, becoming immediately reclined. The two pairs ($1^a + 1^b$, $2^a + 2^b$) are at first united along their dorsal margins but become separated distally so that when the rhabdosome is viewed from the side, the second-order stipes are seen to have a Y-configuration as in *T. phyllograptoides* Strandmark 1902, with an initial 'biserial' portion. In specimens from the 74.7 m level the two stipes are in contact as far as approximately the level of their 8th theca. Their dorsal margins, for a short distance thereafter, are bridged by a sheet of periderm. Stipes in the specimen from the 100.8 m level

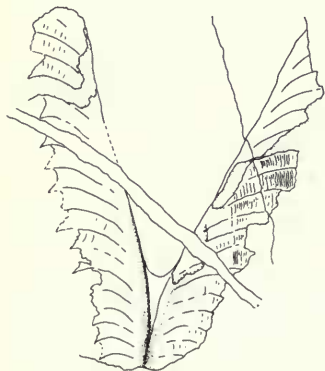


Fig. 21 *Tetragraptus (Tetragraptus) phyllograptoides triumphans* subsp. nov. PMO NF637, incomplete mature rhabdosome preserved in $\frac{3}{4}$ relief showing an a, b stipe pair. From 75 m above base of Olenidsletta Member; $\times 3$.

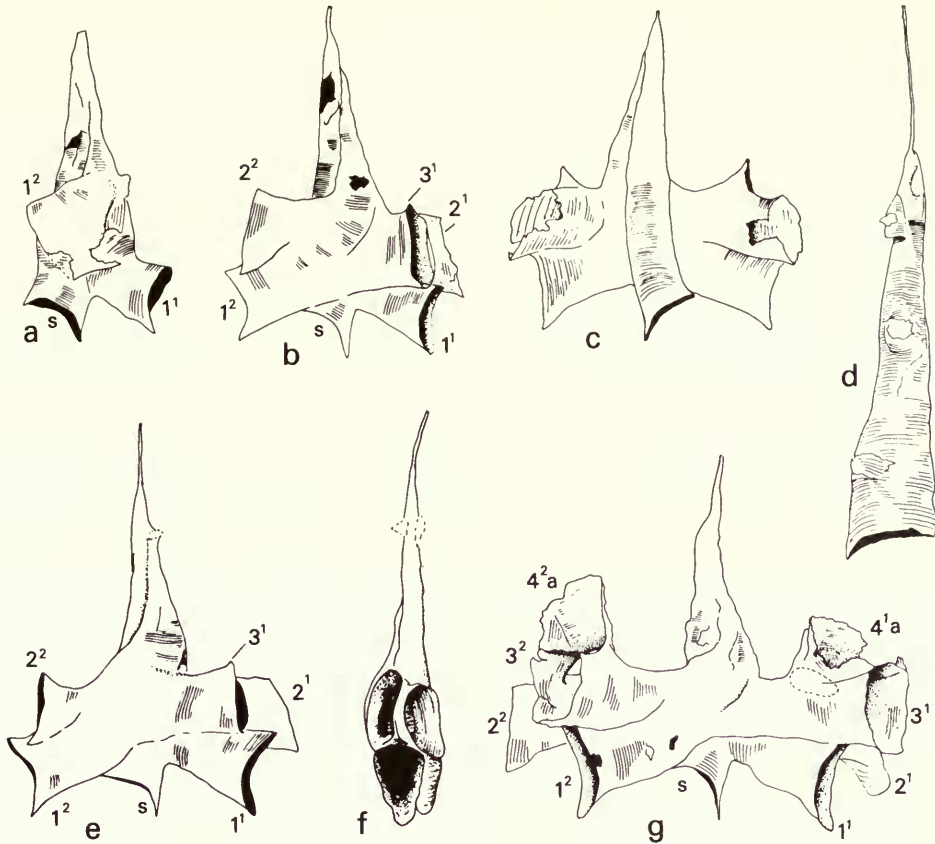


Fig. 22 *Tetragraptus (Tetragraptus) phyllograptoides triumphans* subsp. nov., growth stages. a, PMO NF3180 showing sicula, nearly complete $th1^1$ and beginnings of $th1^2$ and $th2^1$; $\times 20$. b, c, NF3179 and NF3303 respectively, later stages (c, obverse view) showing commencement of growth of $th2^1$, 3^1 and 2^2 ; $\times 20$. In c, note the wider spacing of fusellar rings in the lower wall of $th2^1$ on left, as compared with the closely spaced growth striations seen on the outer surface of all growth stages. d, NF3313, partially grown sicula and initial bud arising on the prosicula; $\times 40$. e, f, NF3178, reverse and lateral (stipe¹ side) views respectively; $\times 20$. g, NF3181, most advanced growth stage recovered, showing commencement of upward growth of second-order stipes; $\times 20$. The foramen opening from $th3^2$ into $th4^2b$ shows on left, and the position of the foramen between $th3^1$ and $th4^1b$ is indicated on the right side of the diagram. The isograptid type of stipe division can be clearly deduced from this specimen. All from 74.7 m above base, Olenidsletta Member, type section.

(NF3182) are in contact up to at least the level of their 12th theca. The angle of divergence of the separated stipes is about 40° ; the angle of intersection of the conjoined portions, as seen in transverse section, is about 120° .

Width of the second-order stipes near their origins is about 2.2 mm, at their point of separation about 3.4 mm and distally about 2.9 mm. Whereas the dorsal margin is convexly curved, the ventral margin is relatively straight, a feature also seen in *Oncograptus* and *Isograptus victoriae maximodivergens*. Maximum length of second-order stipes is over 17 mm.

Thecae are spaced 10–10.5 in 10 mm and are similar to those of *T. serra* from Spitsbergen.

PROXIMAL STRUCTURE AND DEVELOPMENT. Several growth stages have been isolated, of which six are figured (Fig. 22a–g). The apex of the prosicula passes gradually into a short nema or, possibly, the caudal region (Hutt 1974) of the prosicula.

The initial bud arises on the prosicula which is clearly defined in the earliest growth stage recovered (Fig. 22d) and is 0.25 mm in length. Proximal structure is similar to that of

Tetragraptus (Tetragraptus) bigsbyi (Bulman 1970: fig 53). Theca 1¹ grows down the ventral side of the sicula and turns sharply away leaving about 0.3 mm of ventral sicula wall exposed. The sicula aperture is deflected towards the stipe² side of the rhabdosome. Theca 1² arises from 1¹ at a point level with the sicula mid-length. It rapidly expands, and gives off th2¹, the proximal portions of the two thecae forming a broad structure on the reverse side of the rhabdosome as in *T. (T.) serra serra*, though less massive than in that species. The reclined growth of the second-order stipes is already apparent by the third-formed theca on each side (Fig. 22c, e), and strongly developed by theca 4 and 5 (Fig. 22g).

Thecal budding sequence can be clearly deduced from an advanced growth stage (Fig. 22g), and is identical to that of *T. (T.) bigsbyi*. The thecal diagram is given in Fig. 5a, b (p. 174).

Theca 1² is dicalycal and initial development is of isograptid type and dextral mode. In subsequent budding, th3¹ is dicalycal and right-handed, and th3² dicalycal and left-handed. Second-order branching is thus isograptid as in *T. bigsbyi* but second-order pairs of stipes remain united along their dorsal margins.

The thecal budding sequence (development) of the rhabdosome follows the pattern, not only of *T. bigsbyi*, but also of *T. reclinatus toernquisti*, *T. r. reclinatus*, *Pseudophyllograptus angustifolius angustifolius*, and *P. a. chors*, and can be regarded as the standard tetragraptid pattern.

DISCUSSION. The distinctive rhabdosome form, with its two pairs of reclined second-order stipes united at their base, is shared only with one other described species, *T. phyllograptoides* Strandmark, known from the Baltic and Moscow Platform. Swedish forms of the species redescribed by Cooper & Lindholm (in prep.) differ from those of Spitsbergen in their greater number of pendent thecae in the proximal region. In other respects the Swedish form is apparently similar to that of Spitsbergen even to the distance for which the second-order stipes are united. In view of their difference in proximal morphology and of the fact that *T. phyllograptoides* is regarded as a zone fossil for a much lower horizon (zone of *T. phyllograptoides*, Törnquist 1901, Monsen 1937), it seems unwise to include the two forms under the one name. The new name *triumphans* is thus proposed for the Spitsbergen form which is here regarded as a stratigraphic subspecies of Strandmark's (1902) form.

If the partial concrescence of the second-order stipes were carried to completion the result would be a morphological intermediate between *Pseudophyllograptus* and *Tetragraptus*, and if this process were continued so that all four stipes were united the result would be a *Pseudophyllograptus* of *angustifolius* type. The appearance, in Spitsbergen, of *T. phyllograptoides triumphans* immediately before *P. angustifolius chors* subsp. nov. (p. 244) would be consistent with such a derivation for that form. However, the horizontal rather than downward initial growth of thecae 2¹ and 2² matches the later *P. angustifolius angustifolius* from Sweden (Bulman 1936a: fig. 15) more closely than *P. angustifolius chors*, so that the postulated transition would require some structural alteration in the proximal region in addition to change in rhabdosome structure.

Tetragraptus (Tetragraptus) pseudobigsbyi Skevington 1965

Figs 8a, 23a, b; Pl. 5, fig. 7

- 1865 *Graptolithus bigsbyi* J. Hall (*pars*): 86–88; pl. 16, figs 22–24, 27, 28.
- 1964 *Tetragraptus bigsbyi* (Hall) Ge: 397–398; pl. 2, fig. 7?; pl. 3, figs 16–18.
- 1965 *Tetragraptus pseudobigsbyi* Skevington: 8–9, fig. 2.
- 1973 *Tetragraptus pseudobigsbyi* Skevington; Bouček: 20–22; pl. 1, fig. 1; text-figs 3e–g.
- 1976 *Tetragraptus bigsbyi* (Hall); Braithwaite: 28–29; pl. 5, figs 27–32; pl. 12, figs 1–4.

STRATIGRAPHIC RANGE. Olenidsletta Member, 90.8–97 m above base, V₂a.

MATERIAL. PMO NF429, NF431, NF433, NF1580, NF3184.

DESCRIPTION. Rhabdosome of *T. serra* type, but with more strongly reclined stipes. Sicula 2.5 mm long, first-order stipes probably comprised of a single theca each. Details of proximal structure and development unknown. Stipes gently curved or straight distally,

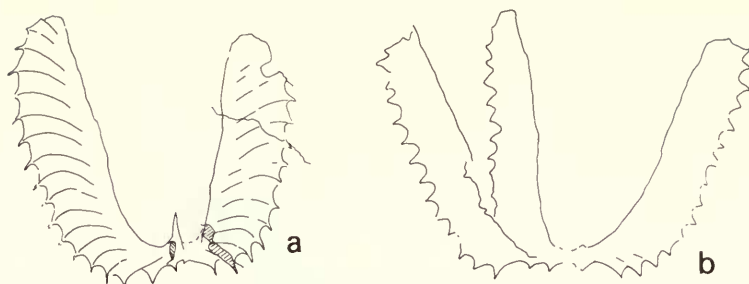


Fig. 23 *Tetragraptus (Tetragraptus) pseudobigsbyi* Skevington. a, PMO NF433, specimen preserved in full relief in limestone; 90.8 m above base, Olenidsletta Member, type section. b, NF3387, flattened specimen possibly belonging here, 22 m above base, Olenidsletta Member, type section. Both $\times 3$.

3.5 mm in maximum width. Thecae of *T. serra* type, spaced 12–13 in 10 mm. Ventral processes protrude prominently, but are not always visible in rock-preserved relief material where they are commonly obscured by matrix.

DISCUSSION. Skevington's (1965: fig. 2) figure of the holotype presents an a,b stipe pair and consequently proximal thecae with a higher angle of inclination than if preserved to show the first order stipes (and sicula) as in our Fig. 23a. In the absence of details of proximal development and structure, the species is distinguished from *T. serra* only in having slightly more strongly reclined stipes and more closely spaced thecae. It probably derived from earlier *T. serra* and should eventually, perhaps, be regarded as a stratigraphical subspecies of *serra*. Poorly preserved specimens from the Profilbekken Member (V_4) differ in having more slender stipes (2.8 mm) and are listed as *T. cf. pseudobigsbyi*.

T. pseudobigsbyi is distinguished from *T. bigsbyi* primarily in having less strongly reclined stipes that are straight or distally reflexed, and on these grounds the specimens described by Braithwaite (1976) from the Wahwah Limestone of early to mid-Arenig age, as *T. bigsbyi*, are here referred to *T. pseudobigsbyi*. Braithwaite described proximal development as isograptid, which might be expected from the close similarity of the species to *T. bigsbyi* in which isograptid development is well known (Bulman 1936a). The forms described as *T. bigsbyi* by Ge (1964), from the Ningkuo Shale of Zhejiang, eastern China, conform more closely with *T. pseudobigsbyi*; the main apparent difference is the wider thecal spacing in the Chinese specimens, given as 10–11 in 10 mm by Ge (1964: 397). However, as measured from his figured specimens, thecal spacing appears to be nearer to 12 in 10 mm.

***Tetragraptus (Tetragraptus) reclinatus reclinatus* Elles & Wood 1902**

Figs 24a, b, 25a–f

1902 *Tetragraptus reclinatus* Elles & Wood: 67, fig. 41; pl. 6, figs 5a–e.

LECTOTYPE. Specimen Q18, figured by Elles & Wood (1902: pl. 6, fig. 5e) and housed in the BM(NH) is here designated as **lectotype** (Fig. 24a).

COMMENTS ON TYPE MATERIAL. Although the species has been widely reported around the world, to our knowledge a lectotype has not previously been designated. We do so here in order to clarify the relationship of Elles & Wood's form to the new material from Spitsbergen. Of the several specimens they figured and now held by the BM(NH), that selected is the best preserved. Both the lectotype (Q18) and the specimen figured by Elles & Wood as pl. 6, fig. 5b (Q20) are refigured here (Fig. 24a, b).

Details of proximal structure cannot be seen in any of the type specimens. The sicula in the lectotype is about 1.8 mm long. The initial two thecae are slightly declined and the second order stipes grow out and up with graceful curvature, becoming straight distally and ending up with a gently reclined attitude. Longest stipes are 18 mm or more long. Stipes expand to their

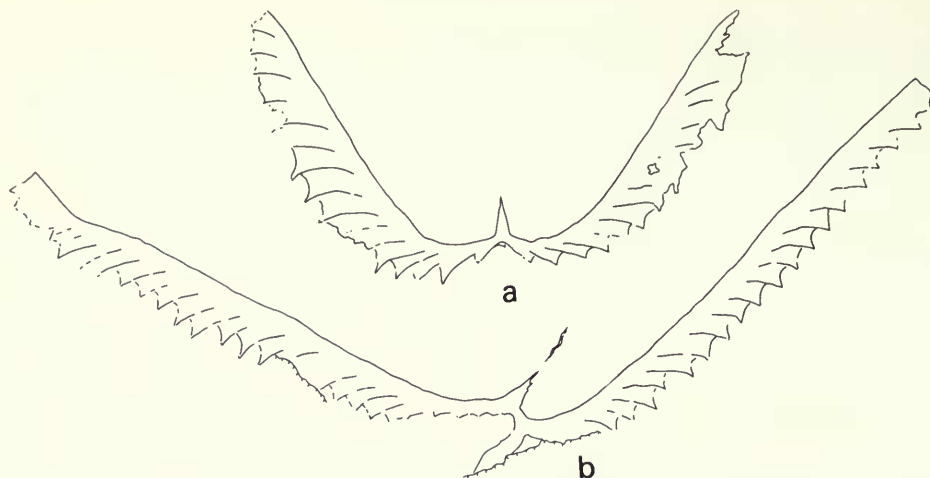


Fig. 24 *Tetragraptus* (*Tetragraptus*) *reclinatus reclinatus* Elles & Wood, type specimens. a, BM(NH) Q18, lectotype; b, Q20, paratype. Figured by Elles & Wood (1902: pl. 6, fig. 5e, 5b respectively). Both $\times 4$.

full width of 2–2.5 mm by about their 7th or 8th theca (Fig. 29). It should be noted that several of the specimens figured by Elles & Wood, including the lectotype, lie outside the maximum value (2 mm) given by them for stipe width. Thecae are spaced 11–13 in 10 mm (12–13 given by Elles & Wood).

The species is distinguished from *Tetragraptus* (*Tetragraptus*) *amii* Elles & Wood (p. 198) by its shorter, more slender (Fig. 29) and less robust second-order stipes, and from *T. (T.) serra* Brongniart by these features and a shorter sicula, and less robust proximal region. Its astogeny is similar to that of *T. (T.) serra* and in morphology it can be regarded as a somewhat less robust version of Brongniart's species.

STRATIGRAPHIC RANGE. 74.7 m level, upper V_1c , Olenidsletta Member.

MATERIAL. PMO NF3304–8.

PROXIMAL STRUCTURE AND DEVELOPMENT. The sicula is 2 mm long, straight and bears a well-developed ventral prolongation of the apertural margin. The preservation is not good enough to allow the prosicula to be distinguished, but a tubular structure, either the cauda or nema, extends from the sicular apex. In the earliest growth stage recovered (Fig. 25a) theca 1¹ arises high on the ventral side of the sicula and grows down in contact with the sicula, then diverges sharply leaving free about 0.25 mm of the ventral sicula wall. The level of origin of th1² and the foramen to th2¹ can be seen in Fig. 25a. From the unconformity in growth striations it is inferred that th1² commences its growth in the form of a dorsal hood, like that of *Xiphograptus formosus formosus* (Bulman 1936a: 24; Skevington 1965: 20) and *X. formosus svalbardensis* (Archer & Fortey 1974: 93). The hood is later linked to the ventral wall (of th1² and 2¹) by fuselli which join it at a relatively high angle. Theca 2¹ grows out over the dorsal wall of th1¹ to open on the obverse side of the rhabdosome; th2² also opens on the obverse side. Subsequent development follows the usual tetragraptid plan, as in *T. bigsbyi*, *Pseudophyllograptus angustifolius* etc. Initial development is thus of dextral mode and isograptid type; th3¹ is dicalycal and right-handed, th3² is dicalycal and left-handed.

LATER GROWTH STAGES. The most complete growth stage is a rhabdosome fragment (Fig. 25e, f) comprising the proximal region and one incomplete stipe. It is sufficient to show that the second-order stipes are gently reclined. Maximum width of the incomplete stipe is 2 mm at the 4th theca. Apertural margins are deeply indented; thecae are moderately curved so that their free ventral margins are inclined to the dorsal stipe margin at 70°–80°.

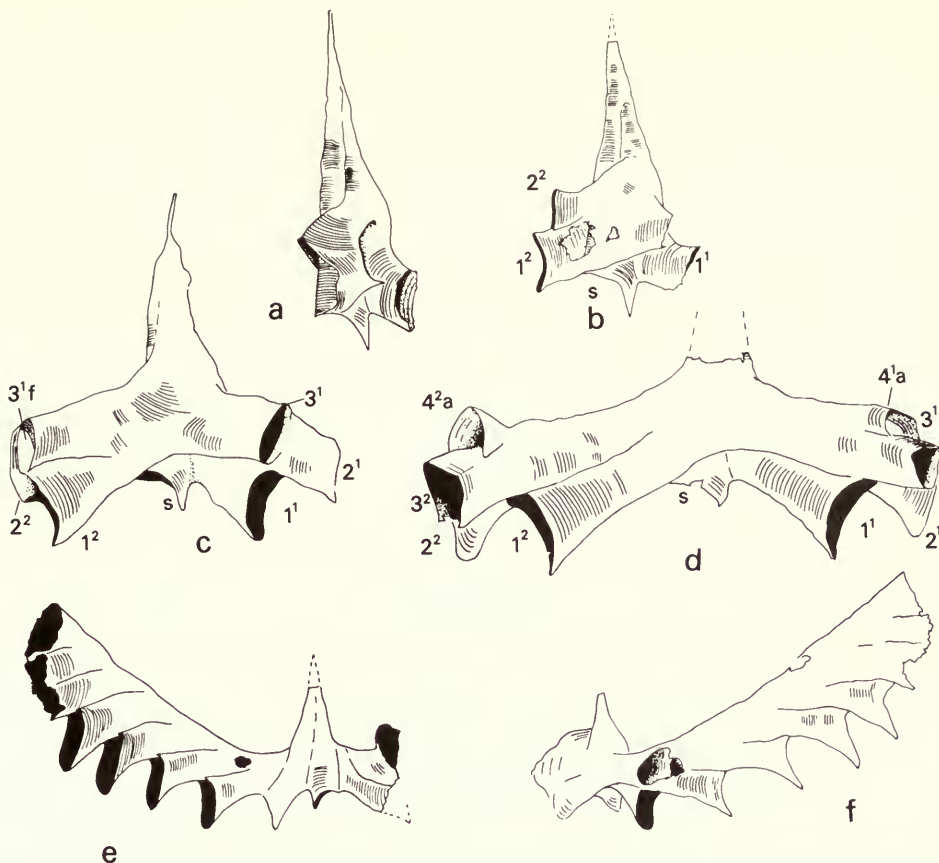


Fig. 25 *Tetragraptus (Tetragraptus) reclinatus reclinatus* Elles & Wood, isolated growth stages from Spitsbergen in which growth of thecae can be inferred from growth striations. a, PMO NF3308, earliest stage showing sicula, partly grown $th1^1$ and incipient development of $th1^2$, with a wide foramen from which $th2^1$ would develop; $\times 20$. The unconformity in growth lines shows clearly. b, NF3307, stage showing the commencement of growth of $th2^1$ (damaged), and $th2^2$; $\times 20$. c, NF3305, later stage in which the wide foramina opening into $th3^1$ and $th3^2$ (3^2f) are clearly displayed; $\times 20$. d, NF750, advanced growth stage from which the budding sequence of the two second-order dichotomies can be inferred; $\times 20$. e, f, NF3305, obverse and lateral-reverse view of proximal region with proximal portion of stipe 'a'; $\times 10$. All from 74.7 m above base of Olenidsletta Member, type section.

DISCUSSION. Although incomplete, the Spitsbergen material is referred to Elles & Wood's species because of its gently reclined stipes and closely comparable stipe expansion rate (Fig. 29). The species' range of morphologic variation is unknown and it is not possible to assess the significance of slight differences in dimensions and curvature in otherwise similar described tetragraptids such as those figured by Cooper (1979: fig. 35). However, the specimens described by Skevington (1965: 10–14) as *T. cf. reclinatus* and *T. cf. serra* have stipes which appear to expand more rapidly than those of *T. reclinatus* as described here.

Tetragraptus (Tetragraptus) cf. reclinatus reclinatus Elles & Wood 1902

Fig. 26a, b; Pl. 4, fig. 11

cf. 1902 *Tetragraptus reclinatus* Elles & Wood: 67; pl. 6, figs 5a–e.

STRATIGRAPHIC RANGE. Olenidsletta Member, 22 m above base, V_1b .

MATERIAL. PMO NF2791, NF3188; flattened specimens.

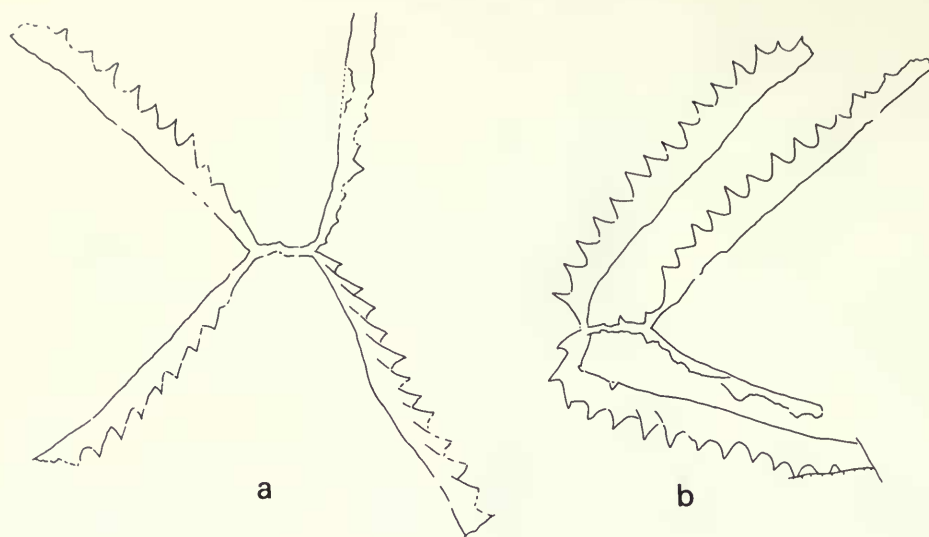


Fig. 26 *Tetragraptus (Tetragraptus) cf. reclinatus reclinatus* Elles & Wood, flattened rhabdosomes. a, PMO NF3188; b, NF2791. Both from Olenidsletta Member, 22 m above base, southern section; $\times 3$.

DESCRIPTION. The sicula is small but its dimensions are unknown. The first-order stipes form a funicle 2.3 mm long. Second-order stipes are up to 18 mm long, straight or slightly curved, concave dorsally. They appear to have been gently reclined so that, as in *T. amii*, they are sometimes preserved in quadribrachiate mode (Fig. 26a) and others in *serra* mode. Stipes reach their maximum width of 1.9–2.0 mm by about their 5th theca. Thecae are moderately curved, and free ventral margins are inclined 50° – 70° . Apertural margins are deeply indented and relatively straight, leaving free a relatively large portion of the ventral wall of the following theca. The ventral stripe margin thus has a characteristically deeply serrated outline.

DISCUSSION. The distinctive feature of the Spitsbergen forms is their deeply serrated stipes, and separates them from other tetragraptids of similar rhabdosome form, such as *T. reclinatus reclinatus* Elles & Wood, *T. r. toernquisti* Monsen (both of which also differ in having more closely spaced thecae), *T. ibexensis* Braithwaite (?= *T. reclinatus* Elles & Wood), *T. amii* Elles & Wood (which also has broader and more rapidly widening stipes) and *Tetragraptus woodae* Ruedemann. There appears to be no suitable name for the Spitsbergen form but the poor quality of our specimens precludes their being used as the basis of a new species. Since they most closely match Elles & Wood's *T. reclinatus* they are listed here as *T. cf. reclinatus*.

Tetragraptus (Tetragraptus) reclinatus abbreviatus Bouček 1956

Fig. 27

1956 *Tetragraptus (Tetragraptus) reclinatus abbreviatus* Bouček: 26; pl. 1, figs 2, 3; text-fig. 8a–d.

1973 *Tetragraptus reclinatus abbreviatus* Bouček; Bouček: 22–23; pl. 2, figs 5–7; text-fig. 3a–d.

STRATIGRAPHIC RANGE. Olenidsletta Member, 20–21 m above base, V₁b.

MATERIAL. PMO NF2392, NF3187.

DESCRIPTION AND DISCUSSION. Small, strongly reclined tetragraptids. Sicula prominent, 2.3 mm long; first-order stipes composed of a single theca each. Second-order stipes 7 mm long and 2.1 mm in maximum width. Thecae are strongly curved, and their free distal margins are inclined at about 90° to the stipe axis. The apertural margins are deeply indented and form an

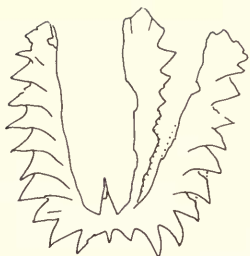


Fig. 27 *Tetragraptus* (*Tetragraptus*) *reclinatus abbreviatus* Bouček. PMO NF2392, 20–21 m above base of Olenidsletta Member, southern section; $\times 4$.

acute angle with the ventral margin, giving a characteristic deeply serrated outline to the ventral stipe margin.

The Spitsbergen specimens match Bouček's figures and description well and correspond with the wider-stiped forms in his population. Bouček's material comes from the uppermost layers of the Klabava Formation (*T. reclinatus abbreviatus* Zone) in beds correlated with the late Arenig, that is, a horizon somewhat higher than that of the Spitsbergen material.

***Tetragraptus* (*Tetragraptus*) *reclinatus toernquisti* Monsen 1937**

Fig. 28a–m

1937 *Tetragraptus toernquisti* Monsen: 161–162; pl. 3, fig. 31; pl. 4, figs 27, 33; pl. 13, figs 1–3.

STRATIGRAPHIC RANGE. 103·3–131 m above base of Olenidsletta Member, V_2 – V_3 .

MATERIAL. PMO NF3189, NF3296–3302, NF3316–8, and numerous other fragmentary specimens, all isolated and in full relief, strongly carbonized; growth lines were revealed in some specimens which partly responded to bleaching in potassium chlorate and nitric acid. PMO NF3221, preserved in shale.

PROXIMAL STRUCTURE AND DEVELOPMENT. The sicula is generally 1·6–1·7 mm long and 0·31–0·33 mm in dorsoventral width at the aperture. It is straight for most of its length; the distal portion, that below the point at which $th1^1$ diverges, is slightly curved towards the dorsal side. The ventral margin of the aperture projects slightly beyond the dorsal margin. Preservation is too poor to allow distinction of the prosicula. Theca 1^1 arises very high on the sicula, follows the same growth path as in *T. reclinatus reclinatus* but diverges from the sicula less sharply. Theca 1^2 commences its growth as a dorsal hood like that inferred for *T. reclinatus reclinatus*. At the same time the lower wall, bridging $th1^2$ and 2^1 (that forming the isograptid arch), is formed as a shelf or plate against the sicula and $th1^1$ (Fig. 28a). The hood apparently ceases growth and the lower shelf is extended up to meet it; at the same time the distal margin of $th1^2$ becomes fully enclosed by the formation of complete half rings. A deep embayment is thus formed (Fig. 28b, c) which eventually is filled in during the formation and growth of $th2^1$. The growth path of $th2^1$ differs from that of its homologue in *T. reclinatus reclinatus* by passing across the sicula and $th1^1$ at a lower level, its ventral wall lying at the level of the junction of the free ventral walls of the sicula and $th1^1$. Subsequent development follows that of the nominate subspecies; $th3^1$ is dicalycal and right-handed and $th3^2$ is dicalycal and left-handed. Initial development is of dextral mode and isograptid type.

LATE GROWTH STAGES. The first-order stipes and proximal parts of the second-order stipes are slightly declined. Second order stipes have similar graceful proximal curvature and gently distally reclined attitude to those of *T. reclinatus reclinatus*. They are proportionately narrower than those of *T. reclinatus reclinatus* (Fig. 29), reaching a width of 1·8–2·1 mm by the 7th or 8th theca, but expand at the same rate. The longest stipe measured is 24 mm long. Thecae are spaced 11–13 in 10 mm in the proximal part of the stipe and slightly wider (down to 10·5 in 10 mm) in the distal part. Thecae are similar in outline and inclination to those of *T. reclinatus reclinatus*.

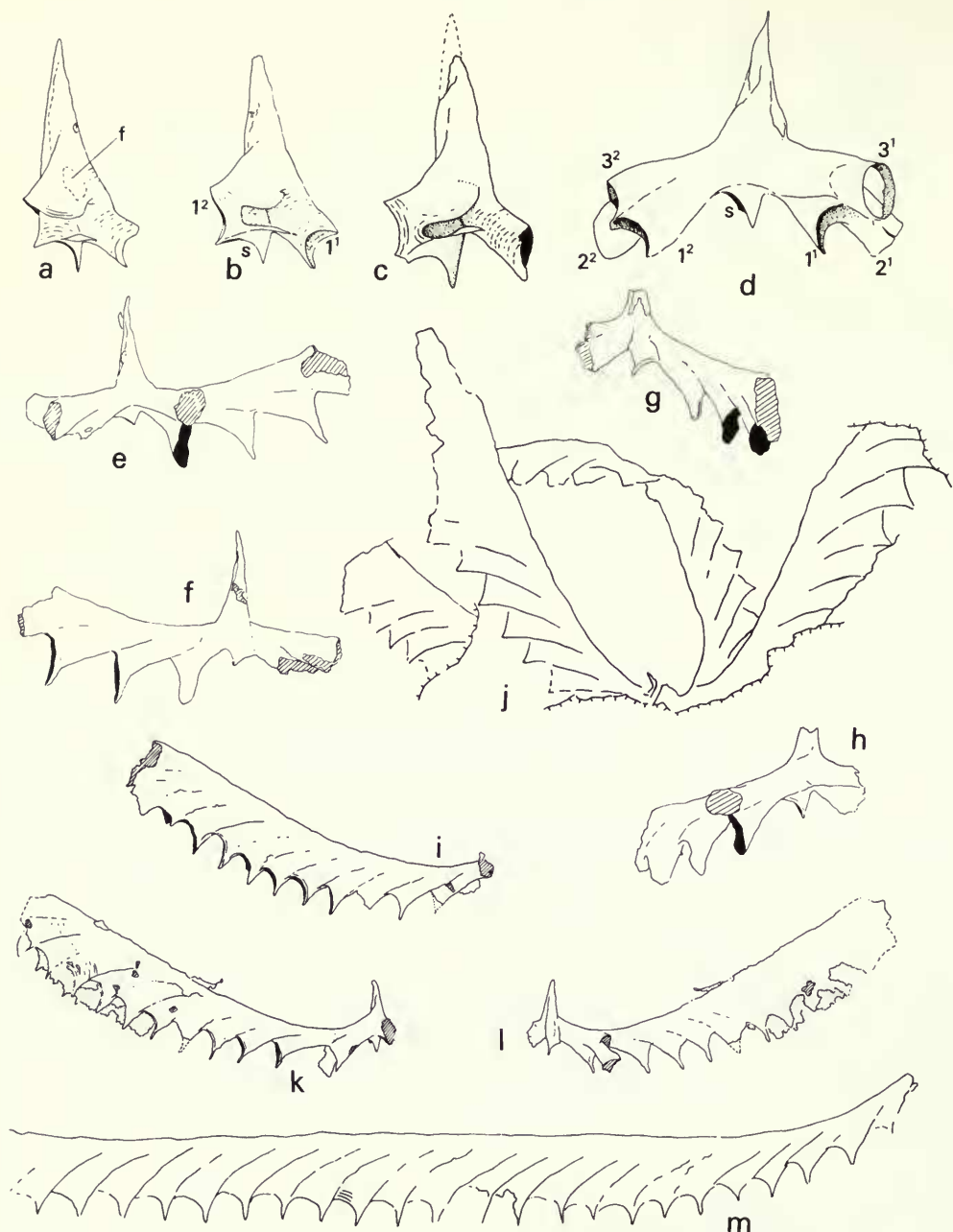


Fig. 28 *Tetragraptus* (*Tetragraptus*) *reclinatus toernquisti* Monsen, isolated growth stages and rhabdosome fragments. a–c, PMO NF3299, NF3298 and NF3317 respectively, successive growth stages showing formation of hood over $th1^2$ and 2^1 , lower 'shelf', and deep embayment formed between these two structures (c), some fuselli visible; $\times 20$. d, NF3301, commencement of second-order dichotomies with dicalycal thecae 3^1 and 3^2 beginning to form; $\times 20$. e, f, NF3297, incomplete proximal end, reverse and obverse views; $\times 10$. g, h, NF3316, incomplete proximal end, obverse and reverse views; $\times 10$. i, NF3318, isolated second-order stipe; $\times 6$. j, NF3221, flattened rhabdosome in shale; $\times 6$. k, l, NF3296, proximal region and stipe $2a$ viewed from reverse side and obverse side respectively; $\times 6$. m, NF3189, incomplete second-order stipe preserved in full relief in limestone; $\times 6$. All from 103.3 m level, Olenidsletta Member, type section, except specimen j which is from 131 m above base of Olenidsletta Member, southern section.

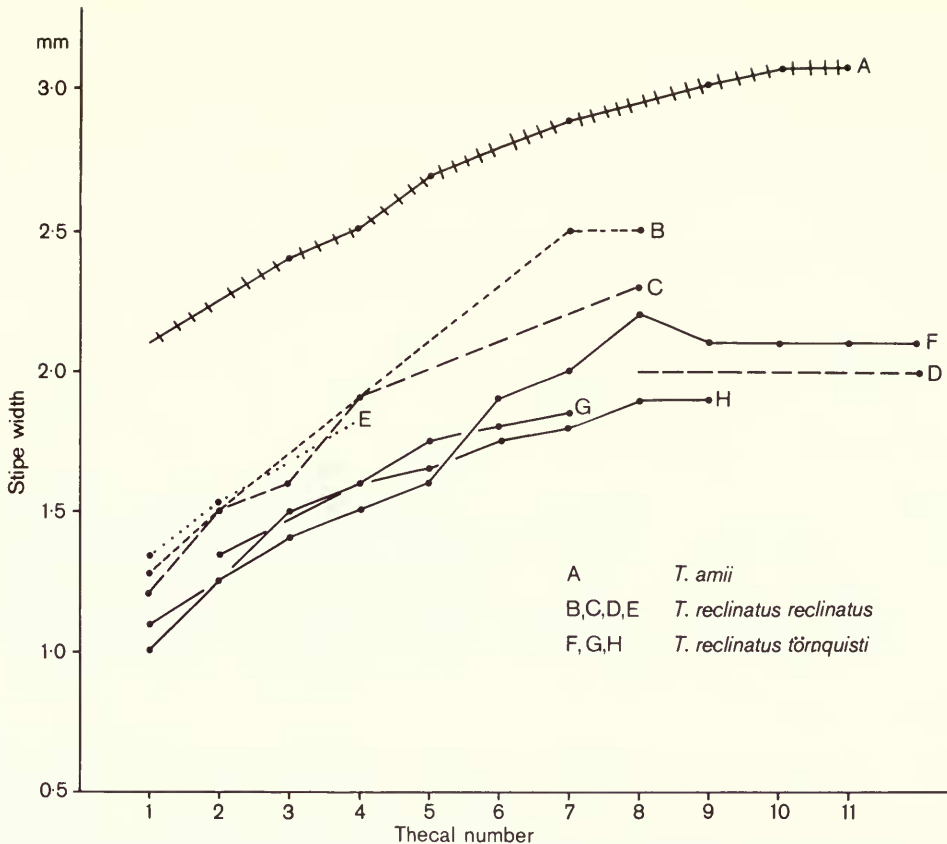


Fig. 29 Stipe expansion curves for second-order stipes of *Tetragraptus* (*Tetragraptus*) species. A, *T. (T.) amii*, PMO NF2817, from Spitsbergen. B–E, *T. (T.) reclinator reclinator*. B, lectotype (BM(NH) Q18); C, paralectotype (BM(NH) Q19); D, paralectotype (Q20), measurements obtainable in distal part only; E, specimen from Spitsbergen (NF3305). F–H, *T. (T.) reclinator toernquisti*, from Spitsbergen. F, NF3189; G, NF3296; H, NF3318. Note that specimens A–D are flattened (shale material), whereas specimens E–H are preserved in relief (isolated material).

DISCUSSION. The subspecies is represented by abundant stipe fragments in our acid-insoluble residues from the 103.3 m level. Most appear to be broken off the rhabdosome shortly after the second dichotomy. Only a single specimen (Fig. 28j) was found preserved in black shale.

The form differs from that referred to *T. reclinator reclinator* in the lower level of its isograptid arch, in the slightly narrower stipes and in its higher stratigraphical position, but there seems little doubt that the two subspecies are closely related.

Monsen's (1937) description of *Tetragraptus toernquisti* is, unfortunately, based on flattened material. From her illustrations the species possessed slightly reclined stipes which become straight distally, rather than horizontal stipes. She gives the following dimensions: stipe width initially 0.4 mm but 'rapidly increasing' to about 1.6 mm; in one example, with stipes 17 mm long, stipe width reaches about 2 mm; thecae are spaced 11–14 in 10 mm. The low value given for proximal stipe width can be expected in flattened shale-preserved material where the full dorsoventral profile of the proximal part of the stipe is not usually seen.

The Spitsbergen material thus appears to best fit Monsen's descriptions and illustrations of *T. toernquisti*.

Among the isolated stipe fragments recovered from samples taken at the 103.3 m level are some which differ from the main population in being somewhat thinner. Whether they

represent a separate population or are merely the thinnest variants of a single variable population is uncertain; they are separated under the name *T. reclinatus* cf. *toernquisti*.

Subgenus *PENDEOGRAPTUS* Bouček & Přibyl, 1951

TYPE SPECIES. *Tetragraptus pendens* Elles 1898.

DIAGNOSIS. Sicula long, slender, wedge-shaped, first theca almost straight, all proximal thecae pendent and proximal region of bryograptid appearance; thecae with projecting ventral apertural margins; up to three orders of consecutive dichotomy, variable in some species.

SPECIES. *Tetragraptus pendens* Elles 1898, *Graptolithus fruticosus* J. Hall 1858, *Tetragraptus clarki* Ruedemann 1902 (?= *T. (P.) fruticosus*), *T. pendens* mut. *posterus* Ruedemann 1947 (= *T. (P.) pendens*), *T. fruticosus* var. *tubiformis* Ruedemann 1904 (= *T. (P.) fruticosus*), *T. fruticosus* var. *campanulatus* Ruedemann 1904 (= *T. (P.) fruticosus*), *T. pendens* var. *praesagus* Törnquist 1901 (?= *T. pendens*), and *Bryograptus crassus* Harris & Thomas 1938.

DISCUSSION. The diagnosis is based on *Tetragraptus fruticosus* (Hall). Until the diagnostic features are confirmed in the type species (*T. pendens* Elles) it, and the subgenus itself, remain provisional. The species here included are confined to strata of Lower Arenig age. Four terminal stipes are the general rule but at least one species, *T. (Pendeograptus) fruticosus*, produces polymorphic variants by the suppression of first one second-order dichotomy (to produce a three-stiped form) and then the second second-order dichotomy (to produce a two-stiped form). Development type has been inferred only in *T. (Pendeograptus) fruticosus* where initial development is dextral and isograptid, and subsequent development, inferred with less confidence, follows the plan of *Tetragraptus (Tetragraptus)*.

The bryograptid appearance of the proximal region of *T. fruticosus* has long been recognized and its derivation from a bryograptid ancestor has been suggested (Elles 1922; see also Ruedemann 1904, Obut 1957). In the *T. (P.) fruticosus* beds of Victoria is found the closest relative of the species, *Bryograptus crassus* Harris & Thomas (1938: 72–73; pl. 1, figs 7a–d; pl. 4, fig. 6). The sicula and thecae are said to be of the same type as those of *T. fruticosus* and (flattened) growth stages of the two forms cannot be distinguished from each other. In *Bryograptus crassus* dichotomies are taken to the third order; the number of terminal stipes ranges from four to six, the four-stiped forms being indistinguishable from slender four-stiped *T. (P.) fruticosus*. Harris & Thomas (1938: 72) state ‘. . . the species seems so closely related to *T. fruticosus*, which occurs in the same bed, that one cannot resist the conclusion that the two forms are genetically related although according to the artificial classification in use they must be placed in different genera’.

Although their figures show that details of proximal structure and sicular morphology are not preserved in the Victorian material, their conclusions concerning relationships seem justified. *B. crassus* is therefore here included in the subgenus *Pendeograptus* and the diagnosis of *Pendeograptus* is framed accordingly. Bithecae are unknown in *B. crassus* and its inclusion in *Bryograptus* was clearly based on the number of terminal stipes and the bryograptid character of the proximal region, thecae, and rhabdosome. The stratigraphic range is given by Thomas 1960 as Lower Bendigonian (Be1), equivalent to the lower part of the range of the four-stiped *T. fruticosus*.

Tetragraptus (Pendeograptus) fruticosus (J. Hall 1858)

Fig. 30a–f; Pl. 3, fig. 4; Pl. 4, fig. 2

1858 *Graptolithus fruticosus* J. Hall: 128.

1865 *Graptolithus fruticosus* Hall; J. Hall: 90–91; pl. 5, figs 6–8; pl. 6, figs 1–3.

1874 *Graptolites (Didymograptus) fruticosus* (Hall) M'Coy: 13; pl. 1, figs 9–14.

1874 *Didymograptus pantoni* Etheridge: 7; pl. 3, figs 21–22.

1902 *Tetragraptus fruticosus* (Hall) Elles & Wood: 61; pl. 6, figs 2a–b.

1935 *Tetragraptus fruticosus* (Hall); Benson & Keble: 275–276; pl. 30, fig. 41; pl. 33, figs 25, 27.

1947 *Tetragraptus fruticosus* (Hall); Ruedemann: 304–305; pl. 51, figs 25?, 26–32.

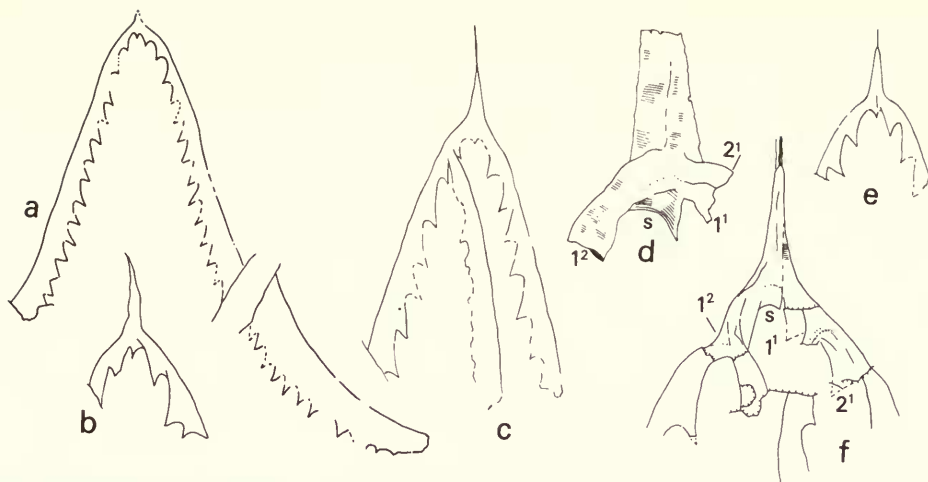


Fig. 30 *Tetragraptus (Pendeograptus) fruticosus* (Hall). a, PMO NF3325, mature two-stiped form, 15–24 m above base of Olenidsletta Member, southern section; $\times 2$. b, NF2836, proximal portion only, 11 m above base of Olenidsletta Member; $\times 4$. c, NF3327, three-stiped form, 9.5–15 m above base of Olenidsletta Member, southern section; $\times 4$. d, SM A105809, incomplete growth stage showing origin of $th2^1$ on 1^2 , isolated but flattened specimen; same horizon as a; $\times 20$. e, NF2852, proximal portion, 18–19 m above base of Olenidsletta Member, southern section; $\times 4$. f, pyritized specimen in shale in partial relief, showing some details of proximal development and structure; from Newfoundland; $\times 6$.

1960 *Tetragraptus fruticosus* (Hall); Berry: 54–55; pl. 6, figs 7, 11, 12; pl. 7, fig. 14; pl. 8, figs 1, 3; pl. 9, fig. 3.

1960 *Tetragraptus fruticosus* (Hall); Thomas: pl. 3, figs 26–28.

1979 *Tetragraptus fruticosus* (Hall); Cooper: 64–65; pl. 6b, e, g; figs 32a–c.

STRATIGRAPHIC HORIZON. Olenidsletta Member, 13–19 m above base, V_1b (both two- and three-stiped forms).

MATERIAL. SM A105809(?), PMO NF2075, NF2836, NF2852, NF3325–7.

DESCRIPTION. The sicula is long and wedge-shaped, ranging from 2.5 to 3.5 mm in length (measured in five specimens). The apex is often difficult to determine, passing smoothly into a nema. The rhabdosome comprises either two or three main stipes – no four-stiped forms are present in the Spitsbergen collections. In the three-stiped form, one first-order stipe (whether stipe¹ or stipe² could not be determined) bifurcates after its first theca to produce two second-order stipes, whereas in the two-stiped form both first-order stipes remain unbranched. The terminal stipes show considerable variation in width and curvature. Most specimens have stipes that are pendent, more than about 2 mm in maximum width, and are no more than about 14 mm in length. A few have long stipes that continue to expand in width, reaching 3–6 mm at about theca 15 (25 mm from the proximal end), thereafter tapering gradually; stipes are reflexed giving the rhabdosome the characteristic bell shape noted by Hall. It is not clear from the Spitsbergen material whether the specimens with shorter slender stipes represent a distinct form or are merely immature growth stages of the larger form. Both forms have two- and three-stiped representatives.

Thecae are strongly denticulate, with deeply recessed apertural margins, resembling in outline those of dendroids. They are spaced 7 to 8 in 10 mm.

PROXIMAL DEVELOPMENT. A few isolated, but flattened, growth stages have been recovered that may represent the species, one of which is figured (Fig. 30d). If correctly assigned it is important because it reveals some details of proximal development. The apices of the sicula and first theca have broken off but origin of $th1^2$ and its initial path of growth are clear. Theca 2^1

originates from 1^2 but it is broken off shortly after its origin along with the distal portion of $th1^1$. The fragment thus shows dextral development of isograptid type, in agreement with that deduced in the Newfoundland specimen described below.

DESCRIPTION OF NEWFOUNDLAND SPECIMEN. A specimen of the slender form of *T. fruticosus* (four-stiped) has been collected from the Cow Head Group of Newfoundland by one of us (R.A.F.) and its description is included here for completeness (Fig. 30f) since it is preserved in partial relief and shows details of proximal development. The sicula is 2.8 mm long, wedge-shaped, and terminates apically in a slender nema which appears to be enveloped in a membrane. Width of the membrane is similar to that of the sicula near its apex. There is no pronounced virgellar projection at the aperture and the ventral side of the sicula is not defined. Theca 1^1 originates high on the sicula, but its point of origin cannot be determined. It is relatively straight, diverging from the sicula at a very low angle, and its aperture lies 0.6 mm below that of the sicula.

The periderm has flaked away in the proximal region of our specimen and the following interpretation is based on the impression remaining, together with the periderm still preserved.

Theca 1^2 arises from $th1^1$ about 0.8 mm above the aperture of the sicula; it grows across the sicula and down assuming a pendent attitude, its aperture lying beneath, and obscured by, the bifurcation of $stipe^2$. Theca 2^2 arises from $th1^2$ in the region of the sicula aperture and follows a sinuous growth path (probably accentuated by flattening of the rhabdosome). The origin of $th2^1$ is not preserved but from an impression in the lower part of the sicula it is probable that a second 'crossing canal' was present and $th2^1$ is therefore likely to have originated from $th1^2$ rather than from $th1^1$.

Subsequent development of the rhabdosome is a little obscure and two interpretations are possible for the origin of second-order stipes on both the $stipe^1$ and $stipe^2$ sides. In the most probable interpretation for the $stipe^1$ side, $th2^1$ grows out along the right-hand stipe shown in Fig. 30f, $th3^1$ is dicalycal and $th4^1b$ is given off producing a dichotomy that is right-handed and isograptid. However, because the origin of $th3^1$ is not clearly defined, it is possible that the growth path of $th2^1$ is misinterpreted above, and that instead it grows along the left-hand stipe; $th2^1$ would then be the dicalycal theca and the dichotomy would be of *artus* type.

Similarly, on the $stipe^2$ side, the most probable interpretation is that $th3^2$ is given off from $th2^2$ at the level of the aperture of $th1^2$; it grows out along the left-hand stipe shown in Fig. 30f, and is dicalycal, giving rise to $th4^2b$ which grows down the right hand stipe, thus producing a dichotomy that is of isograptid type (whether of right- or left-handed mode is uncertain). A possible, but less probable, interpretation would have $th2^2$ as dicalycal, producing a dichotomy of *artus* type.

In the favoured interpretation, development of the rhabdosome follows the general plan of other tetragraptids with all dichotomies of isograptid type and dicalycal thecae separated, in budding succession, by normal unicalycal thecae. However, should either, or both, of the alternative interpretations for the two second-order dichotomies hold true, then *T. fruticosus* would depart significantly from the general tetragraptid plan, and occupy a unique place among the dichograptids in having first isograptid, then *artus* type dichotomies in succession (see, however, *Didymograptus* (*Didymograptellus*) *multiplex* sp. nov. described below, p. 229).

DISCUSSION. The significance of the two rhabdosome forms, that with pendent narrow stipes and that with broad reflexed stipes, is not clear. Hall's (1865) illustrations show that both forms were present in his material and both forms are present in Australia (Thomas 1960) and New Zealand (Cooper 1979). It is clear that in some cases at least (e.g. the New Zealand material) the slender form could not represent an immature stage of the broad reflexed form, since its stipes are pendent and straight beyond the point of reflection in the reflexed form. However, from the literature, there appears to be considerable variation in the level at which the stipes become reflexed. In the New Zealand form (Cooper 1979: fig. 32a, 4-stiped) they commence their recurvature at about the level of $th8-9$, in the Australian form of Thomas (1960: pl. 3, fig.

28a, 3-stiped) at about th11–12, in New York specimens of Ruedemann (1947: pl. 51, figs 26–32) at th11–12 (in 3- and 4-stiped forms referred to 'variety *tubiformis*') and th20–24 (3- and 4-stiped forms of 'variety *campanulatus*'), and in Quebec specimens of Hall (pl. 6, figs 1–3, 3- and 4-stiped) at about th12–14. Pending a review of the species all forms are here retained within it.

Two-stiped forms of *T. fruticosus* have long been known in Australia (Etheridge 1874, Thomas 1960) but to our knowledge have not been recorded from elsewhere. However, they are closely similar to the forms described as *Didymograptus v-fractus* Salter by Elles & Wood (1902: 33–35; pl. 2, figs 10a–b) and may well be present elsewhere recorded under Salter's name. The two species are certainly closely similar. From their description and illustrations Elles & Wood's material differs in having a somewhat shorter sicula (2–2.5 mm), slightly more closely spaced thecae, stipes that do not attain the full width of 3.5 mm of the broad reflexed *T. fruticosus*, and apertural margins that are less recessed resulting in less conspicuously denticulate thecae. However, the question needs further examination before the relationship between the two forms can be assessed.

Etheridge (1874) figured Victorian specimens of the two-stiped form under the name *Didymograptus pantoni*? M'Coy, and listed in his synonymy of *D. pantoni* a reference to Salter 1863. In fact neither M'Coy nor Salter figured or described the form and authorship of the name *pantoni* must be attributed to Etheridge. The name has not generally been used by subsequent Australasian workers (e.g. Keble & Benson 1939, Thomas 1960) who have regarded it as a synonym of *T. fruticosus* (Hall).

In Australia and in Spitsbergen, the two-stiped form has a similar range to that of the three-stiped form. The two-stiped form can be derived from the three-stiped form by suppression of the second dichotomy. Although not clear in the Spitsbergen material, the third-formed stipe in three-stiped forms was found to be developed on the stipe¹ side in New Zealand material (Cooper 1979) and the three-stiped form was thus regarded as being derived from the four-stiped form by suppression of the last dichotomy (that based on stipe²). It therefore follows that all three forms (two-, three-, and four-stiped) of *T. fruticosus* can be regarded as polymorphic variants of a single species (Cooper 1979: 64) in which there is a change in morph frequency with time; four-stiped forms appear first, then two-, three- and four-stiped forms together, and two- and three-stiped forms only are found at the top of the range. The change in frequency with time has been employed for stratigraphic subdivision of early Arenig sequences (Thomas 1960, Berry 1960, 1962).

TETRAGRAPTUS Salter 1863, *sensu lato*

Tetragraptus contrarius sp. nov.

Fig. 31a–d; Pl. 3, figs 2, 3

STRATIGRAPHIC RANGE. Mid-part of Olenidsletta Member, V₂, 90–97 m from base; top of the Arenig *Didymograptus bifidus* Zone (Ca₁).

DIAGNOSIS. Robust, reflexed *Tetragraptus* with mature stipe width 4–6 mm. Strong dorsal-convex curvature of stipe unique among tetragraptids, producing long thecae with initially low inclination, highly curved distally, and overlapping as far as long apertural lips. Distal thecal spacing 10–12 in 10 mm.

MATERIAL. **Holotype**, PMO NF2648. Other material (paratypes): PMO NF2631, SM A109728–30.

NAME. 'Contradictory', referring to the unusual stipe form.

DESCRIPTION. This is a sufficiently distinctive species to warrant naming it on relatively little material. Even separate stipes are immediately recognizable. This is because the stipes, after their initial dorsal flexure, are curved in a fashion opposite to all other tetragraptids of which we are aware, being markedly convex along the dorsal side, so that the thecae are crowded together on the concave side. The degree of curvature varies: on the holotype it is marked near the proximal end and decreases distally, but on other specimens the stipe continues to curve

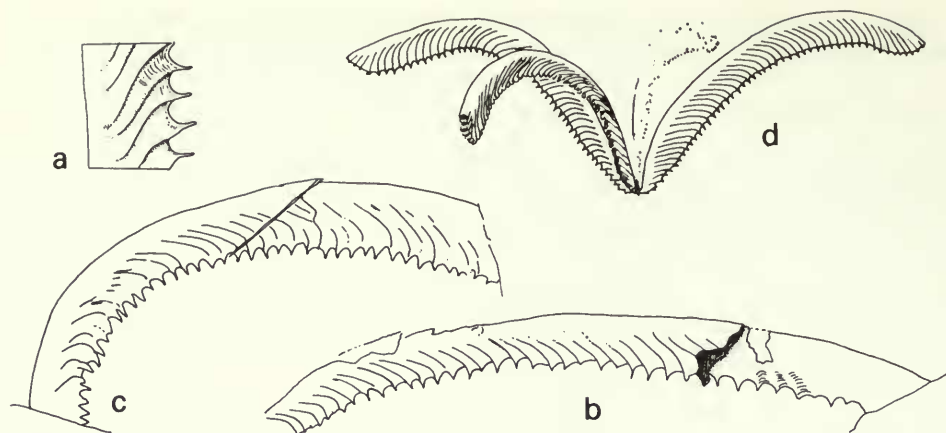


Fig. 31 *Tetragraptus contrarius* sp. nov. a, b, SM A109728, portion of stipe to show thecae ($\times 3$) and full, gently curved, stipe (incomplete; $\times 2$) respectively. c, A109729, well-preserved typically curved stipe; $\times 2$. Both from Profilstranda, Olenidsletta Member, V₂a, 9 m above base. d, reconstruction of rhabdosome assuming moderate curvature of stipes; $\times 1$.

fully through a quarter circle (Fig. 31c). Width of stipes is variable, ranging from 4 to almost 6 mm, and there is little change along the stipe, so that as in *T. serra* there is no taxonomic importance to be attached to thinner- or thicker-stiped variants. No proximal ends are well preserved, but it is possible to deduce that the initial thecae had low inclination, and that there was an abrupt narrowing of the stipes in the proximal region (? first two or three thecae of each stipe) much like the robust forms of *T. serra*. Some lengths of stipe in limestone are preserved in full relief, showing that the stipes had a rather narrow cross-section, about 0.8 mm across. Thecae initially with rather low (30°) inclination to dorsal wall, bending often abruptly near their apertures to become nearly normal to the dorsal wall. Apertures appear excavated deeply on flattened material, with long denticles forming a series of spines normal to the dorsal stipe margin. Well-preserved material shows that the thecal apertures are actually prolonged into spoon-like lips, 0.6 mm long or slightly more, the apertural margins being slightly concave (Fig. 31a). Distance between apertural lips is 1 mm or slightly less, resulting in a thecal spacing of 10–12 in 10 mm.

DISCUSSION. The distinctive habit of this species distinguishes it from all other *Tetragraptus* species. A few specimens described elsewhere, particularly *Tetragraptus denticulatus* of Hall (1865: pl. 4, fig. 13), show a gentle reflection like some of the less extreme stipes in our collection. Hall's species has narrower stipes (3 mm or less) and only about 8 thecae in 10 mm distally. Flattened material from New Zealand attributed to *T. headi* (J. Hall) by Cooper (1979: pl. 9, fig. c) shows a curious twist in the stipes near the proximal end; distal to this a stipe profile is presented, which is slightly convex in the manner of our species, but no apertures are visible in the proximal part. Such an appearance might result from plan-view flattening of species with *T. contrarius* morphology. If the proximal part were strongly recurved as in our species flattening may present us with a near-dorsal view of the stipes with no apertures visible; distally the stipes would have to bend to present a profile. In other features the New Zealand material compares with the narrowest of our specimens; it is from a younger horizon (zone of *I. victoriae maximodivergens*).

Tetragraptus cf. *hsui* Ge 1964

Fig. 32

cf. 1964 *Tetragraptus hsui* Ge: 385–386, 399–400, text-figs 5a–b; pl. 3, figs 1–4.

STRATIGRAPHIC RANGE. Olenidsletta Member, 20–21 m above base, V₁b.



Fig. 32 *Tetragraptus* cf. *hsui* Ge. PMO NF2389, Olenidsletta Member, V₁a, 20–21 m above base, southern section; $\times 4$.

MATERIAL. PMO NF2389.

DESCRIPTION AND DISCUSSION. Very small reclined tetragraptid. Sricula 1.7 mm long, first-order stipes probably of one theca each. Details of proximal development and structure unknown. Second-order stipes reach 1.4 mm wide by the level of their third theca and are only about 4 mm long. Thecae are relatively straight; measurements of their spacing are rather meaningless in such a small form.

Although not well preserved, the tiny size of the Spitsbergen form is distinctive and the general similarity of its rhabdosome, and thecal, form to Ge's figures of *T. hsui* (Ge 1964: text-figs 5a, b) from the Ningkuo Shale is striking. However, the Chinese form is associated with *Cardiograptus* and comes from a higher horizon (approximately latest Arenig). In view of this, and the paucity of the Spitsbergen material, we list the Spitsbergen form as *T. cf. hsui*.

Tetragraptus kindlei Ruedemann 1947

Fig. 33

- 1947 *Tetragraptus kindlei* Ruedemann: 306; pl. 50, figs 6–11.
 1964 *Tetragraptus harti* Ge: 393; pl. 1, fig. 14; text-fig. 2.
 ?1973 *Tetragraptus kindlei* Ruedemann; Bouček: 23–25; pl. 1, figs 5–7; text-fig. 4a–d.
 ?1976 *Tetragraptus pogonipensis* Braithwaite: 30–31; pl. 8, figs 15–17, 19–21; pl. 14, figs 1–7.

STRATIGRAPHIC HORIZON. Olenidsletta Member, 20–21 m above base, V₁b.

MATERIAL. PMO NF2386.

DESCRIPTION AND DISCUSSION. The apex of the sricula is broken away, the apertural position projects slightly below the ventral margin of the 'funicle'. The first-order stipes together reach 3 mm in length and are comprised of a single, long, slender theca each. They appear to be slightly dependent. The second-order stipes are gently curved, becoming straight distally and were probably gently reclined in the original rhabdosome. The free walls of ventral thecae are inclined at a low angle (20°–30°).

The Spitsbergen specimen matches Ruedemann's description and illustrations well. *T. kindlei* was described from the *G. dentatus* Zone of the Glenogle Shale, British Columbia. The long, narrow initial thecae resemble those of species here referred to Subfamily Sigmagraptinae, but without the complete sricula this cannot be confirmed. The specimen from the Ningkuo Shale figured by Ge (1964: pl. 1, fig. 14) as *Tetragraptus harti* closely matches the Spitsbergen form.



Fig. 33 *Tetragraptus kindlei* Ruedemann. PMO NF2386, incomplete mature rhabdosome. Olenidsletta Member, V₁b, 20–21 m; $\times 4$.

The specimens from the Arenig of Bohemia described by Bouček as *T. kindlei* have a relatively long, narrow sicula and clearly isograptid development type. However, they have slightly closer thecal spacing (10 in 10 mm) and less curved second-order stipes, which appear to have been slightly declined or horizontal rather than reclined. They are therefore only tentatively included in the species here. *Tetragraptus pogonipensis* Braithwaite (1976: pl. 8, figs 15–17, 19–21; pl. 14, figs 1–7), from the Wahwah Limestone (mid Arenig), appears to have a similar overall rhabdosome morphology and a development type described as isograptid. However, its initial thecae are shorter and stouter than those of specimens here referred to *T. kindlei*, producing a shorter and broader ‘funicle’.

Tetragraptus quadribrachiatus (Hall 1858)

Pl. 4, figs 13, 14

- 1858 *Graptolithus quadribrachiatus* J. Hall: 125.
 1865 *Graptolithus quadribrachiatus* Hall; J. Hall: 91–92; pl. 5, figs 1–5; pl. 6, figs 5, 6.
 1902 *Tetragraptus quadribrachiatus* (Hall) Elles & Wood: 57–58; pl. 1a–e.
 1979 *Tetragraptus quadribrachiatus* (Hall); Mu *et al.*: 52; pl. 16, figs 6–9.
 1979 *Tetragraptus quadribrachiatus* (Hall); Cooper: 66; pls 56, 96.

STRATIGRAPHIC HORIZON. 8·8–15 m above base of Olenidsletta Member, V₁a.

MATERIAL. PMO NF3319–20 and a few fragmentary specimens.

DESCRIPTION AND DISCUSSION. First-order stipes together form a ‘funicle’ 2 mm long; they appear to be comprised of a single theca each. Second-order stipes expand gradually in width and are straight and arranged more or less at right angles to each other. Full dorsoventral stipe width unknown as only the dorsal aspect can be seen. Thecal details unknown.

Tetragraptus quadribrachiatus has been widely reported around the world and apparently has a long time range. However, it is poorly known and the name may well embrace forms belonging to more than one species. The Spitsbergen material conforms to Hall’s description in gross rhabdosome morphology. Although not well preserved, the first-order stipes appear to comprise a single theca each, as in most other tetragraptids. Ruedemann’s (1947) claim that the first-order stipes of specimens from Deep Kill assigned by him to *T. quadribrachiatus* possess two thecae each would indicate that development of the rhabdosome did not follow the standard tetragraptid plan and his specimens may therefore not belong to Hall’s species.

Other tetragraptids

A few Spitsbergen collections contain tetragraptids that are either too poorly preserved or too incomplete to allow definite identification.

Collections from the 125–130 m level (V₃) contain numerous fragments of stipes, up to 70 mm long, preserved in full relief. In only one specimen was the proximal region present allowing determination of the rhabdosome as that of a strongly reclined tetragraptid. Stipe width ranges from 2·9 to 3·4 mm and thecal spacing is 9–11 in 10 mm. The material possibly represents Ge’s (1964) species *T. rigidus* but comparison is difficult owing to discrepancies between Ge’s description and illustrations. For example, maximum stipe width is given as 4·3 mm (3·2 mm in one specimen) whereas, from his figured specimens, values of 3·0–3·5 mm seem more common. Similarly, thecal spacing is given as 7–8 in 10 mm (6 in 10 mm distally) whereas spacing measured off two of the figured specimens (one of which is the holotype) is 9–11 in 10 mm. Thus dimensions of the Spitsbergen specimens lie within the range of *T. rigidus* as determined from Ge’s illustrations but differ somewhat from those given in his text. Because of this uncertainty, and the absence of information on the sicula and proximal structure of the rhabdosome, the Spitsbergen material is listed here as *T. rigidus*?

Genus *DIDYMOGRAPTUS* M’Coy, 1851

TYPE SPECIES. *Graptolithus munchisoni* Beck 1839.

CLASSIFICATION of ‘*Didymograptus*’. Bouček (1973: 128–135) presented a general discussion of

the principles of classification of dichograptoids in which he states several times that their 'generic differentiation . . . depends on their phylogenetic relationships' (p. 134). Such a putative view has been adopted, explicitly or implicitly, in a number of earlier accounts (Bouček & Přibyl 1951, Jaanusson 1960, Obut 1964). The old genus *Didymograptus* M'Coy has long been recognized as a form-genus which is likely to be polyphyletic (e.g. Nicholson & Marr 1895; Bulman 1936a), and in the last edition of the *Treatise* Bulman (1970: fig. 75) clearly indicates different phylogenetic routes by which graptoloids of *Didymograptus* grade might be derived.

This awareness of the polyphyletic nature of *Didymograptus* has led to the proposal of a number of genera purporting to be 'natural' groups of species. These include *Expansograptus* Bouček & Přibyl 1951, *Corymbograptus* Obut & Sobolevskaya 1964 and *Acrograptus* Tzaj 1969. These 'genera' formerly subsumed within *Didymograptus*, are based on gross rhabdosomal form; *Didymograptus*, *sensu stricto* constitutes the 'tuning-forks' with *D. murchisoni* as type species, *Expansograptus* includes extensiform species with *D. extensus* as type species, *Corymbograptus* deflexed forms with *D. v-fractus* as type species, and *Acrograptus* declined species with *D. affinis* as type species. These 'genera' are little more than upgraded versions of Elles & Wood's (1901) informal divisions. Bulman (1970) rejected these generic concepts, a rejection that Bouček (1973: 134) seems to interpret as a repudiation of the principle that dichograptid graptoloids ought to be classified phylogenetically. In practice what ought to be challenged is whether the characters taken as diagnosing the 'genera' are of any phylogenetic significance whatsoever. Curiously, Bouček (1973: 129–130) seems to reject proximal end development and structure as a criterion for classification in dichograptoids, and didymograptids in particular, on the presumption that because certain kinds of development were subject to natural selection, they were not of fundamental taxonomic importance. He goes on to show that *distal* characters, such as stipe width or thecal overlap, also vary in a species-to-species way, and were also therefore subject to low-level selection pressure. The basis for the presumption that gross rhabdosomal form is indicative of real phylogenetic links is not critically examined.

The material which can be isolated from the Arenig of Spitsbergen has cast new light on the importance of proximal structure in the classification of didymograptids. Complex proximal end characters indicate that truly phylogenetic classification not only splits up the old form-genus *Didymograptus*, but also cuts across the defined limits of the new, supposedly phylogenetic, genera. Bulman's caution in accepting *Expansograptus* and the like seems to have been fully justified. For example, we describe below a stratigraphic species lineage extending from '*Didymograptus*' *elongatus* to '*D.*' *formosus* in which a consistent and unusual proximal end structure is present (in this case the origin and growth of th1' on the antivirgellar side, when most contemporary graptoloids do not even have a virgella), while the gross rhabdosomal form changes from that supposedly characteristic of *Expansograptus* to that of *Acrograptus*. In this case the new 'genera' are unequivocally as much form-genera as was the old genus *Didymograptus*, and ones, moreover, without the partial justification of long historical usage. Within *Didymograptus*, *sensu stricto* (tuning-fork graptolites) there is evidence of a cluster of species of Arenig age in which the proximal end development is of isograptid type. The so-called *bifidus* stage ('dichograptid type') of development of Bulman (1936a) is based on Llanvirn material (wrongly attributed to *D. bifidus* Hall), where there is again a cluster of pendent species with similar development. Since the species from these different horizons are in almost all other respects perfect homeomorphs there is really no other recourse here but to regard the proximal end development as of fundamental phylogenetic importance.

As so often the case with graptoloids, the great majority of described didymograptids are known from flattened and imperfect type material. The form-genera at least permit a classification of these forms more finely than simply lumping them all as *Didymograptus*, but the point of so doing, if this does not reflect a phylogenetic grouping, is obscure: as they have similar ranges no stratigraphic purpose is served. However, there is a need to divide *Didymograptus* into monophyletic groups of species.

What we propose here is essentially a compromise. The form-genus *Didymograptus* is retained, specifically for those species of which proximal details cannot be determined. Monophyletic divisions of the genus are for the moment accorded subgeneric status. The names *Acrograptus*, *Corymbograptus* etc. are validly proposed, but they will have to be redefined in terms of the detailed structure of their type species before their use or otherwise in a phylogenetic classification can be assessed. The stipe attitude by itself is rejected as a basis for definition of groups.

Pendent didymograptids

The taxonomic state of the pendent didymograptids is in great confusion. The characters which have been generally employed are few; they are: 1, length of the sicula; 2, width of the stipes, and their rate of expansion from the proximal end; 3, thecal spacing; 4, acuteness of the thecal apertures; 5, divergence of the stipes; 6, thecal inclination. Not all these characters are independent of one another. Overall rhabdosome size has also been used, and larger size invariably accompanies thicker stipes with longer thecae (greater overlap) and higher distal thecal inclination. Most populations at any one horizon exhibit variation in these characters. It is bewildering to find that there has been a proliferation of new species names in the last few years (Braithwaite 1976, Bouček 1973, Mu *et al.* 1979); the last-named paper proposed 23 new species of pendent didymograptids without reference to the other two papers, in which seven new species were erected. Apart from the species proposed in the three papers listed above, pendent didymograptids include the following species (and this list is probably not exhaustive):

Didymograptus acutus Ekström 1937, *D. amplus* Elles & Wood 1901, *D. artus* Elles & Wood 1901, *D. bidens* Keble 1927, *D. bifidus* (Hall 1865) (and subspecies *latus* Ruedemann 1947), *D. bigcanyonensis* Decker 1944, *D. canadensis* Ruedemann 1947, *D. chapmani* Decker 1944, *D. chrbinensis* Bouček 1973, *D. clavulus* Perner 1895, *D. columbianus* Ruedemann 1947, *D. denticulatus* Berry 1960, *D. filiformis* Tullberg 1880, *D. flagellifer* Törnquist 1901, *D. furcillatus* Lapworth 1875, *D. geminus* (Hisinger 1840) (and subspecies *latus* Ekström 1937), *D. halli* Bouček 1932, *D. incertus* Perner 1895, *D. indentus* Hall 1858, *D. liber* Monsen 1937, *D. mendicus* Keble & Harris 1934, *D. minutus* Törnquist 1879 (and subspecies *pygmaeus* Monsen 1937), *D. miserabilis* Bulman 1931, *D. munchisoni* (Beck 1839) (with several named 'varieties', e.g. by Ekström 1937), *D. nanus* Lapworth 1875, *D. pacificus* Ruedemann 1947, *D. pakrianus* Jaanusson 1960, *D. pandus* Bulman 1931, *D. paraindentus* Berry 1960, *D. pendulus* Harris & Keble 1932, *D. protoartus* Decker 1944, *D. protobifidus* Elles 1933 (and subspecies *praecursor* Monsen 1937), *D. protogeminus* Decker 1944, *D. protoindentus* Monsen 1937, *D. protomunchisoni* Decker 1944, *D. rozkowskiae* Kozłowski 1954, *D. smithvillensis* Berry 1970, *D. spinulosus* Perner 1895, *D. stabilis* Elles & Wood 1901, *D. turneri* Decker 1944, and *D. vacillanoides* Perner 1895.

This makes a grand total of about seventy species or subspecies of pendent didymograptids. Given the few characters available, and the variation in populations, it is difficult to see how so many taxa can be justified; there has been little in the way of population studies on the group. Earlier ideas about increase in size and robustness of the rhabdosome during the Llanvirn must now be modified, because giant, *munchisoni*-like species now seem to be found at all the earlier horizons as well, for example, from the early (Mu *et al.* 1979) or the mid (Berry 1970) Arenig. Continued thecal and stipe growth is evidently a polyphyletic character, and may even prove to be of less than specific significance in some lineages.

There has been no previous attempt to divide this pendent series of species into smaller generic units; Bouček (1973) evidently considered the pendent habit defined a monophyletic group. The type of *Didymograptus*, *sensu stricto* is *D. munchisoni*. Some species of pendent *Didymograptus* from the Llanvirn have th1¹ dicalycal at the *artus* (= what Bulman called *bifidus*, p. 171) stage of development; *D. artus* Elles & Wood (Skwarko 1967), *D. sp. nov.* aff. *minutus* (Skevington 1965: 24) and *D. rozkowskiae* Kozłowski 1954 all described from isolated material, where the evidence is unequivocal. Bouček (1973) cites further examples with th1¹ dicalycal, which are less convincing as they are known only from flattened material, and which include at least five Llanvirn species, and two (*D. minutus minutus* and *D. chrbinensis*) from

Arenig strata. These last are very slender species and our experience with *Sigmagraptus* (below) indicates that very well-preserved material is necessary to be certain of the development of such forms. In any case it is certain that there is a cluster of species from Llanvirn localities with $th1^1$ as the dicalycal theca. In these species $th1^1$ also originates low down on the sicula, well below the prosicula and often low on the metasicula.

The concept of *Didymograptus*, *sensu stricto* has perforce to be based on *D. munchisoni*, the type species. Unfortunately, the development of *Didymograptus munchisoni* is not known from isolated material. Bulman (1936a: 84) showed $th1^1$ dicalycal but in his accompanying text attributes the development to the *minutus* stage. Subsequently the *minutus* stage (Bulman 1970: 74) became a division of the isograptid type of development (i.e. with $th1^2$ dicalycal), but Bulman did not state whether he believed that *D. munchisoni* should now be regarded as having $th1^2$ dicalycal. Re-examination of the type series of *D. munchisoni* is not very helpful; all that can be said of the specimens, which have a little relief, is that *none* show the isograptid arch. To this we would add that British material termed *D. bifidus* (non Hall 1865) has $th1^1$ dicalycal, and *D. munchisoni* is clearly related to this form and may be no more than a stout variant of it. Another related species, *D. pakrianus* Jaanusson 1960, also probably has $th1^1$ dicalycal, and some specimens of *munchisoni* from Abereddy Bay are extremely close to *pakrianus* itself. Taken together this evidence suggests that the type species of *Didymograptus* had a proximal end development like that of *D. artus* and Welsh material commonly (and incorrectly) termed *D. bifidus* has $th1^1$ dicalycal.

Well-preserved isolated specimens of what we believe to be the true *Didymograptus bifidus* (Hall) show a perfect isograptid development, with $th1^2$ dicalycal (Fig. 34a, b). In this case $th1^1$ has a high, possibly prosicula origin which has the effect of broadening the pyramid formed by the sicula + proximal thecae (sicula 'wedge') as seen in flattened material. Some of our pendent Arenig forms have this type of sicula 'wedge'. Braithwaite (1976) had previously remarked on isograptid development in flattened pendent *Didymograptus* from Utah. There thus appears to be a cluster of Arenig species with isograptid development.

It therefore seems reasonable to introduce a taxonomic distinction between the two main types of development. For those pendent didymograptids with isograptid development and an

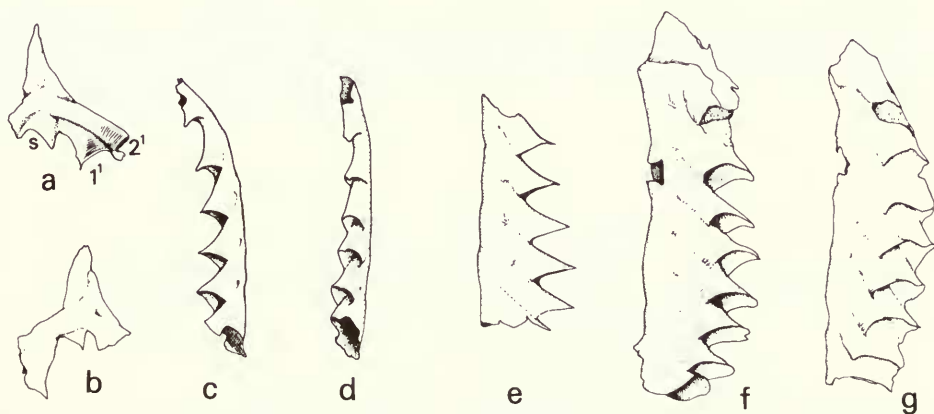


Fig. 34 *Didymograptus* (*Didymograptellus*) *bifidus* Hall. a, b, PMO NF3345, NF3346 respectively; $\times 16$. Isolated proximal portions, reverse views: note isograptid arch and origin of $th2^1$ near proximal part of $th1^2$, proving the assignment to *Didymograptus* (*Didymograptellus*). c–g, isolated stipe fragments from same horizon as a and b to show change in thecal form along stipe; all $\times 8$. c, d, NF728, proximal part of stipe from $th1$, two views. e, NF734, mid part of stipe. f, g, NF748, distal part of stipe showing transverse thecal apertures (specimen slightly crushed proximally); the right hand view shows how thecae may become imbricated during flattening. All 75 m from base of Olenidsletta Member on Profilstranda.

origin of $th1^1$ high on the sicula we introduce the new subgenus *Didymograptus* (*Didymograptellus*). In contrast to Bouček (1973) we regard it as probable that *Didymograptus* (*Didymograptus*) and *Didymograptus* (*Didymograptellus*) are phylogenetic groups. The utility of this distinction is shown by the fact that the European specimens of what has been called *D. bifidus* (and gives its name to the zone) has *artus* development, whereas if we are correct in our determinations true *D. bifidus* is a *Didymograptellus* species. This would put to an end the excessively protracted debate about whether the North American and European zones of *D. bifidus* can be correlated on the basis of the eponymous species.

Subgenus *DIDYMOGRAPTELLUS* nov.

TYPE SPECIES. *Graptolithus bifidus* Hall 1865.

DIAGNOSIS. *Didymograptus* with pendent habit, rhabdosome gracile to robust. Theca 1^1 typically originates high on sicula, and of similar length to sicula. Theca 1^2 dicalycal, with normal isograptid development.

NAME. Diminutive of *Didymograptus*.

DISCUSSION. The proximal end development distinguishes *Didymograptellus* from *Didymograptus* in the restricted sense. This inevitably leaves many pendent species for which the proximal structure is not fully known, and for these the generic name *Didymograptus* has to be used *sensu lato*. It is now clear that the development of *Didymograptus* (*Didymograptus*) with $th1^1$ dicalycal is not primitive, but a derived condition with only a few known exemplars (Cooper & Fortey 1982). *D. (Didymograptellus) multiplex* sp. nov., described below, indicates a mechanism by which the *artus* type of development can be derived from the isograptid type. In flattened material there are obvious problems in distinguishing the two types of development. Where $th1^1$ grows down beside the sicula this broadens the cone at the apex of the flattened rhabdosome with angles of about 25° – 30° ; in *Didymograptus* (*Didymograptus*) species with low metasicular origin of $th1^1$ the sicula looks markedly acute, with an apical angle of about 10° – 15° . Any tectonic distortion removes such discriminating characters.

Although the high sicular origin of $th1^1$ is typical of *D. bifidus* we also include in *Didymograptellus* those species, like *D. minutus*, which retain isograptid development, but apparently with a low sicular origin of $th1^1$.

INCLUDED SPECIES. *Didymograptus bifidus* (Hall 1865); *D. minutus* (Törnquist 1879), *D. fillmorensis* Braithwaite 1976 and *D. millardensis* Braithwaite 1976. Most of the forms identified in the past as *Didymograptus protobifidus* Elles 1933 probably belong here. The subgenus ranges from the North American subcontinent, through Spitsbergen to northeastern Russia, China, Australia and New Zealand. The *minutus* stage species are found in Scandinavia.

Didymograptus (Didymograptellus) bifidus (Hall 1865)

Figs 34a–g, 35f; Pl. 5, figs 11, 12

- ?non 1858 *Graptolithus bifidus* Hall: 130 (*nomen dubium*; ambiguous description, no figure).
- 1865 *Graptolithus bifidus* Hall (*pars*): 73–74; pl. 1, figs 16–18; non pl. 3, figs 9, 10.
- non 1870 *Didymograptus bifidus* (Hall) Nicholson: 346, fig. 7.
- ?non 1875 *Didymograptus bifidus* (Hall); Lapworth in Hopkinson & Lapworth: 646; pl. 33, fig. 8.
- non 1901 *Didymograptus bifidus* (Hall); Elles & Wood: 42–44; pl. 4, fig. 1.
- 1904 *Didymograptus bifidus* (Hall); Ruedemann: 689–692; pl. 15, figs 1–3.
- non 1931 *Didymograptus* aff. *bifidus* (Hall); Bulman: 33, fig. 10; pl. 12, figs 6, 7.
- non 1937 *Didymograptus bifidus* (Hall); Ekström: 26, pl. 2, figs 9–14.
- 1944 *Didymograptus bifidus* (Hall); Decker (*pars*): 382, figs 31, 32; ?non figs 29, 30.
- ? 1944 *Didymograptus protoartus* Decker: 384, fig. 4.
- 1947 *Didymograptus bifidus* (Hall); Ruedemann: 327–328; pl. 54, figs 11–16.
- 1947 *Didymograptus columbianus* Ruedemann: 329; pl. 54, figs 25–29.
- non 1950 *Didymograptus bifidus* (Hall); Phillipot: 241.
- 1960 *Didymograptus bifidus* (Hall); Berry: 59; pl. 10, figs 3, 7–10.

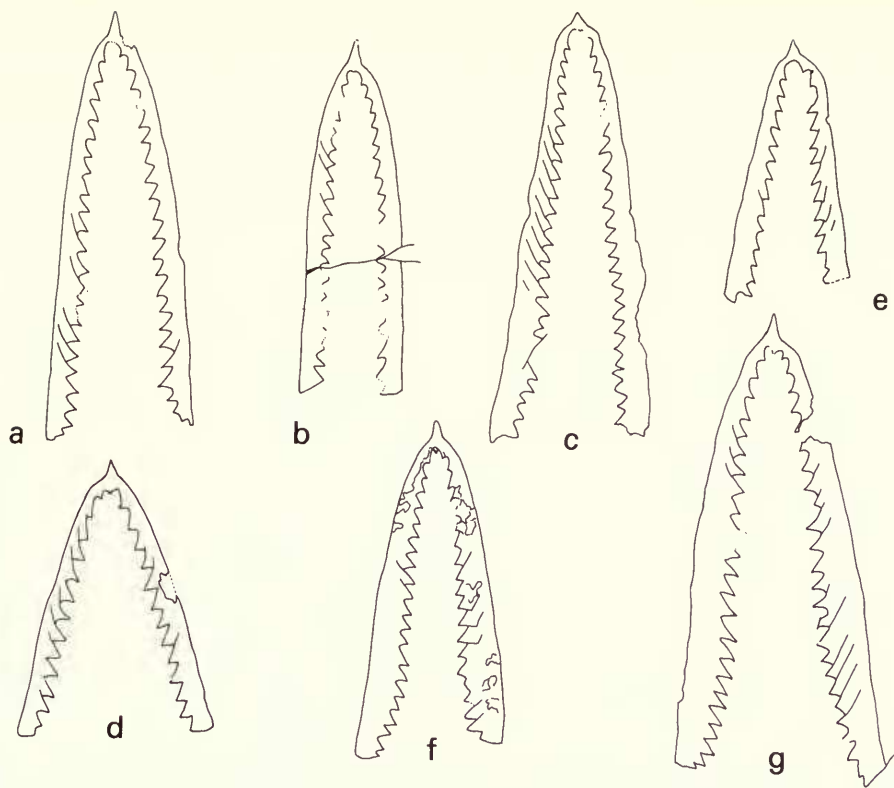


Fig. 35 Flattened didymograptids of the *Didymograptus* (*Didymograptellus*) *bifidus* – ‘*protobifidus*’ morphological group. a–d, *D. (D.)* ‘*protobifidus*’ Elles. a, SM A105812, typical example, close to holotype; type section, 57 m from base of Olenidsletta Member. b, holotype, Skiddaw Slates, English Lake District, BM(NH) Q7. c, PMO NF657, large example transitional in morphology with *D. (D.) bifidus*; about 70 m from base of Olenidsletta Member on Olenidsletta. d, NF824, specimen with stipes splayed more widely than usual, 35 m from base of Olenidsletta Member on Profilstranda. e, *D. (D.)* cf. *meitanensis* Chen, NF2849, 17 m from base of Olenidsletta Member, Profilstranda. f, *D. (D.) bifidus* Hall, specimen GSC 56912 from Hall’s type population, close to the specimen of Fortey (1976: text-fig. 3b). g, *D. (D.) diapason* Chen & Xia, NF834, 35 m from base of Olenidsletta Member. All $\times 3$.

- 1960 *Didymograptus bifidus* (Hall); Thomas: 17 (older Australian records are *D. protobifidus*, fide p. 27).
 1962 *Didymograptus bifidus* (Hall); Berry: 294–297, text-fig. 1a–d.
 1970 *Didymograptus bifidus* (Hall); Berry: 64, figs 1b, c, f, 2c.
 non 1973 *Didymograptus* cf. *bifidus* (J. Hall 1865); Bouček: 98–101; pl. 15, fig. 8; text-fig. 31.
 1976 *Didymograptus bifidus* (J. Hall); Fortey: 274–275, text-fig. 3.
 ? 1979 *Didymograptus bifidus* (Hall); Mu *et al.*: 70; pl. 23, figs 11–15.

STRATIGRAPHIC RANGE. 75 m to 93 m from base of Olenidsletta Member on type section; sporadic through V_2 on Olenidsletta outcrops; total range from V_{1c} to V_{2a} (Arenig; *D. bifidus* Zone).

MATERIAL. Specimens additional to those given in Fortey (1976: 274) include isolated proximal ends PMO NF3345–6, distal isolated stipes NF728, NF734, NF748, relief specimens on rock NF621 and NF2031 (slender form).

DESCRIPTION. This species has already been discussed by Fortey (1976), who showed that specimens from Spitsbergen could be matched with those from the Marathon region, Texas,

which form the basis of the zone of *D. bifidus* in North America. We have now succeeded in isolating some relief material, which merits further description. Isolated proximal ends are mostly of mature specimens, thickened with secondary periderm. The sicula is 1.0–1.2 mm long, measured from the base of the very short nema, which does not exceed 0.2 mm in length. The aperture of the sicula is extended on the ventral side into a short, rounded lip about 0.2 mm long. The sicular aperture is oval, its long axis in the median plane of the rhabdosome being 0.30–0.35 mm long, the shorter axis about two-thirds of this. Theca 1¹ originates within 0.2 mm of the top of the sicula, and is closely similar to the sicula in shape and dimensions, its long axis making an angle of about 30°–35° with that of the sicula, and its free ventral wall extending at least 0.4 mm away from the lower part of the sicula. The divergence of the sicula and th1¹ occurs about 0.2 mm above the base of the sicula on its ventral side. Budding of th1² is near the top of th1¹, and its downward growth across the sicula to form the second stipe is such as to make an approximate right angle with th1¹. Total length of th1² is about 1.3 mm. Theca 2¹ originates within 0.2–0.4 mm of the top of th1², forming an obtuse angle with it as it curves over the back of th1¹ to form the second stipe. Proximal width of th2¹ is about 0.2 mm. The arch formed by the ventral walls of the proximal parts of thecae 1² and 2¹ in reverse aspect is a conspicuous feature of the relief material, but since it passes above the embayment between the sicula and th1¹ it would not necessarily be seen on severely flattened material. Theca 1² is dicalycal and the distance between the proximal parts of th2¹ and th2² is about 0.6 mm, so that the two daughter thecae are well separated. Proximal thecal apertures are, like the sicular aperture, elongate oval in the dorsoventral (sagittal) plane. In the population from which the isolated material has been obtained the stipes widen rather rapidly, and as the thecae increase in length so the apertures become progressively more transverse, finally becoming transversely elliptical at about th20. The distal stipe fragments are very robust, the transverse width being 1.1 mm where the dorsoventral stipe width is 1.9 mm. The distal thecal apertures are strongly excavated, the apertural margin making an angle of 30°–40° with the ventral wall of the theca. The mid-part of the apertural margin is prolonged into a short lip, which appears in flattened material as a tiny denticle. Note that the interthecal septa are slightly shorter than the free dorsal wall on distal material, and may be slightly curved; at their inner ends they make distinct dimples in the exterior rhabdosome wall. Isolated distal fragments have about 16 thecae in 10 mm, and we have observed little change in thecal spacing along the stipes.

COMPARATIVE REMARKS. The isolated material comes from a horizon 75 m from the base of the Olenidsletta Member, low in the range of the species. As noted by Fortey (1976), the early population here tends to have stipes that diverge at up to 30°, a higher angle than that noted by Berry (1962) in his description of the four specimens of *Didymograptus bifidus* from the type locality. However, there are specimens from only a little higher in Spitsbergen which have distal stipe divergence as low or lower than type *D. bifidus* (Pl. 5, fig. 11), and this character is so variable that no importance is here attached to it. Hall's types are not well enough preserved to show development but they clearly show the short 'paired' structure of sicula and th1¹ that typifies our isolated material. There is a complete transition between *Didymograptus* (*Didymograptellus*) *bifidus* and *D. (Didymograptellus) 'protobifidus'* which underlies it in the Olenidsletta Member (Figs 36, 37), but the earlier species merits taxonomic recognition because it is clear that there is a change at the population level between the two, and one which is of stratigraphical importance. The simplest difference to use is the distal thecal spacing, 12–13 in 10 mm in the typical '*protobifidus*' populations and 14–16 in 10 mm in typical *bifidus* populations. Closer thecal spacing pertains even in individual specimens of *D. bifidus* which are otherwise more like *D. 'protobifidus'* in stipe attitude and thecal expansion rate. Fig. 37 shows the gradients obtained from the straight line fits on the stipe expansion diagram, which shows a shift in the populations as a whole towards higher gradients (= greater increase in width of stipe per theca) from '*protobifidus*' to *bifidus*. It is obvious that there is stratigraphical overlap between populations of the two species, and specimens with thecal spacing 13–14 in 10 mm distally and with stipe expansion gradient of about 1.5 should best be referred to as '*protobifidus*'–*bifidus* transitions. Hall's type populations and others from Quebec seem to

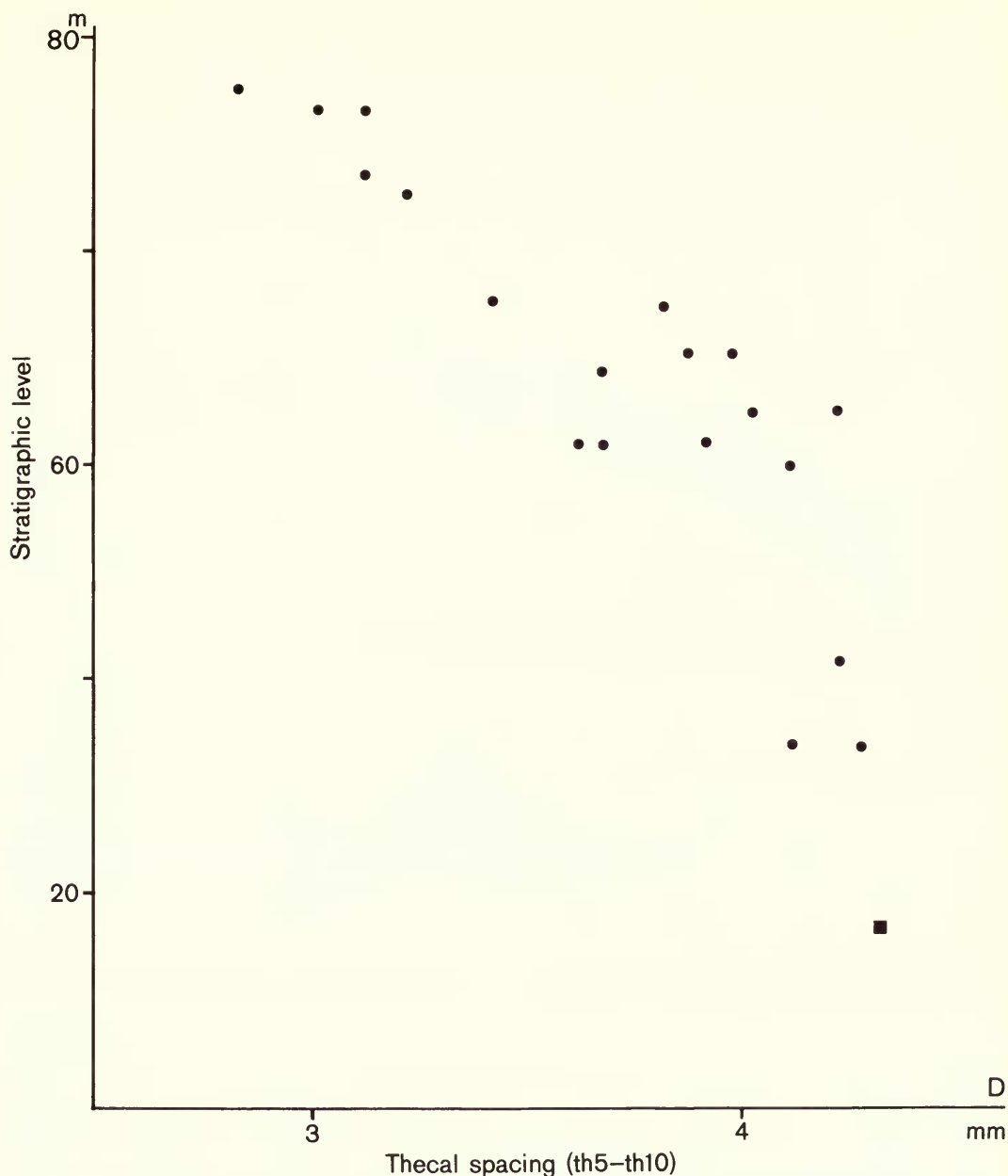


Fig. 36 *Didymograptus* (*Didymograptellus*) 'protobifidus' to *D. (D.) bifidus* series, plot of thecal spacing against stratigraphic occurrence in metres from base of Olenidsletta Member. Spacing is taken as distance from the apertural denticle of th5 to that of th10 as standard. Square at 17 m is for *D. (D.) cf. meitanensis* Chen.

include forms which are like typical Spitsbergen *bifidus* as well as some that may be 'protobifidus'–*bifidus* transitions: in other words the type population may be from a horizon low in terms of the range of *D. bifidus* in Spitsbergen. Hall's population occurs along with other extensiform didymograptids and phyllograptids which prove its Arenig age. Since *D. 'protobifidus'* has distal thecae with the apertures less deeply excavated than those of *D. bifidus*, so that the angle of the apertural margin to the ventral wall of the theca is 45°–50°, it is expected

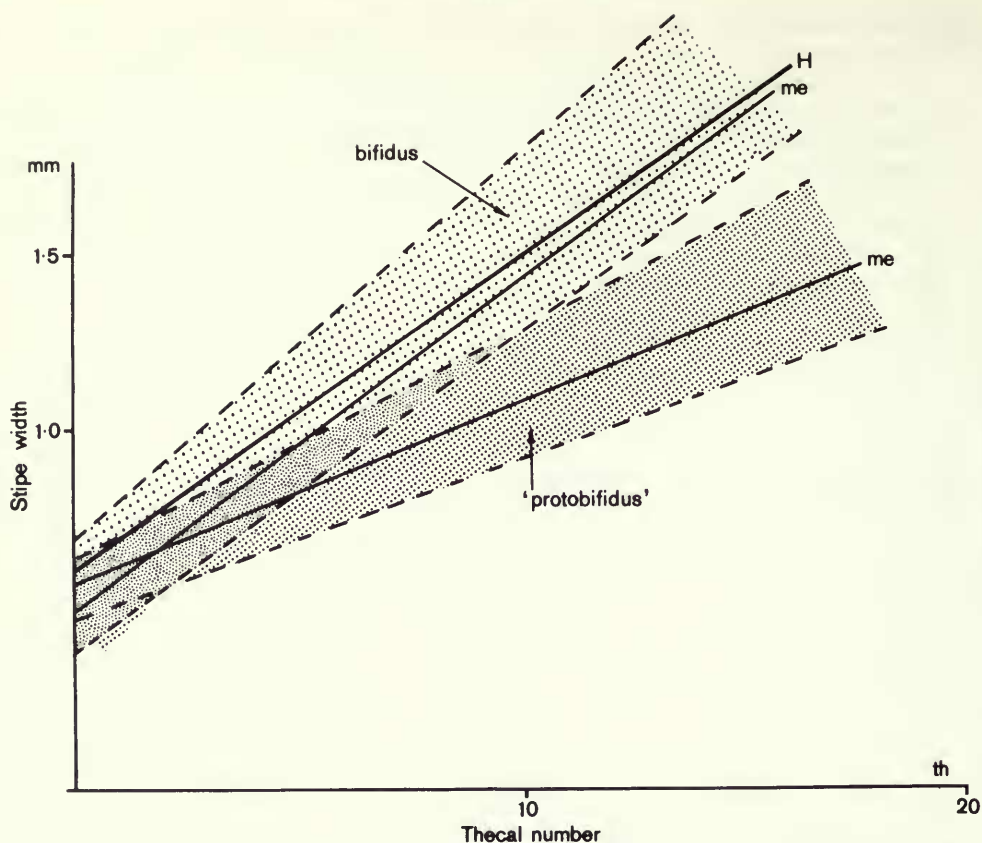


Fig. 37 Stipe expansion diagram for the populations *Didymograptus* (*Didymograptellus*) 'protobifidus' to *bifidus*. Spread of calculated regressions for the populations of these two stratigraphically intergrading species from the Valhallfonna Formation. Dense stippling shows 'protobifidus'; light stippling shows *bifidus*; me – median regression line for both species. H is the regression for the specimen of *D. bifidus* from Hall's type population illustrated in Fig. 35f.

that the distal thecae of *D. 'protobifidus'*, when eventually found in relief, will be found to retain more of the character of the proximal thecae they more closely resemble, i.e. elongate rather than transverse apertures.

The British material that has been referred to *D. bifidus* has $th1^1$ dicalycal rather than $th1^2$, and is therefore not conspecific, but distal thecal and stipe characters are very similar to those of *D. bifidus*, *sensu stricto*. Another difference is that the British material, when well-preserved, shows a long, narrow and gently tapering sicula, for which lengths of 1.5–2.0 mm are common. Unlike North American *D. bifidus* the nema is not clearly differentiated from the sicula. The low origin of $th1^1$ can also be seen on some British specimens having partial relief, but this detail is obscured when the specimens are preserved as a white film, as at Abereiddy Bay. Obviously, a different name has to be applied to the British specimens, of which *D. spinulosus* Perner 1895 may be the senior.

A welter of pendent *Didymograptus* species have been described from China by Mu *et al.* (1979). In south-west China a zone of *D. deflexus* (which is not the time equivalent of the zone of the same name in Britain as shown on their p. 11) is divided into several subzones, partly on the basis of pendent didymograptids. The occurrence in this same interval of true *Phyllograptus* (as restricted in this paper – p. 273) is good evidence of its contemporaneity with the 'protobifidus'–*bifidus* interval in Spitsbergen. Most of these species seem to have been based on

a holotype-to-holotype comparison with previously described species, and preservation is not adequate to determine proximal end structure. The species identified as *D. bifidus* apparently occurs stratigraphically *underneath* a species identified with *D. protobifidus* in south-west China; if we are correct in deducing a continuous transition from *D. 'protobifidus'* to *D. bifidus* in Spitsbergen, one or other of the determinations from China must be incorrect. Many of the other species supposedly endemic to south-west China – *D. eobifidus*, *D. subtilis*, *D. cf. protoartus*, *D. meitanensis* and *D. wudangensis*, for example – may prove to fall into the range of variation shown in the series '*protobifidus*' to *bifidus*, and without further information on the intraspecific variation in the populations of pendent species from south-west China the taxonomic status of these species must be viewed with caution. But it is important to note that the Chinese pendent didymograptids are divided into two groups stratigraphically, one Arenig and the other Llanvirn, separated by a gap. The earlier of the two may be those with isograptid proximal end development, the later with th1¹ dicalycal.

Braithwaite (1976) has a similar gap in Utah between pendent species of Arenig age and one of probable Llanvirn age. However, he has determined the latter as *D. bifidus*, which is puzzling, now that European Llanvirn *bifidus*-like forms have been shown to belong to a different species on the basis of their proximal end development. The sicula attributed to the species by Braithwaite (1976: pl. 16, fig. 2) cannot belong to it, as it clearly shows the long virgella characteristic of the Phyllograptidae. Braithwaite states that the *D. bifidus* from Utah has isograptid development, but this cannot be clearly seen from the figured specimen. The origin of th1¹ appears lower on the sicula (1976: pl. 16, fig. 4) than is the case in our *D. bifidus* and the prosicula is extended into a tube. These differences may be enough to suggest that the Utah form is a different species.

D. bifidus in the restricted sense (with the possible exception of the Utah specimens) seems to be confined to Arenig rocks of the Pacific province, corresponding broadly with the Ordovician equatorial regions: Texas (Berry 1960), Quebec, Newfoundland, Spitsbergen, south China and the Canning Basin, Western Australia furnish specimens which can be definitely assigned. Oddly enough, in what might be termed the classic 'black shale' graptolite facies (Australia, New Zealand, western Ireland, Yukon, and western facies in the Basin Ranges of Idaho) it appears to be lacking, although '*protobifidus*' is present. It seems that there may have been some facies control on its appearance, and it may prove to be confined to the more inshore of Arenig successions.

Didymograptus (Didymograptellus) diapason Chen & Xia in Mu *et al.* 1979

Fig. 35g

1979 *Didymograptus diapason* Chen & Xia in Mu *et al.*: 68; pl. 22, figs 7–15.

STRATIGRAPHIC RANGE. Olenidsletta Member, V₁b, 35 m from base in type section, middle Arenig (*D. protobifidus* Zone).

MATERIAL. PMO NF824, NF834.

DESCRIPTION. The name *Didymograptellus diapason* is applied to a small population of stout 'tuning-forks' from low in the Olenidsletta Member, which are essentially similar to *D. 'protobifidus'*, but in which the stipes distally attain a much greater thickness. The sicular 'wedge' shows the broad cone characteristic of the *bifidus*–'*protobifidus*' group as a whole (length 1.3–1.5 mm) and presumably consists of the sicula and th1¹ growing downwards together. The proximal two or three thecae on each stipe are similar to *D. 'protobifidus'*, but thereafter the stipes thicken up to a marked degree, so that on the stipe expansion diagram (Fig. 38) the gradients are much steeper than in that species. Our specimens do not reach the length of some of the Chinese type population, but the rate of stipe expansion is identical to that given by Chen & Xia (*in* Mu 1979: 68), such that at th15 the width is 2.1 mm. Thecal inclination (so far as it is visible on our rather poor material) remains constant at about 40°, even when the stipes become quite thick. The free dorsal wall of the thecae at th5 is 0.8–1 mm long and remains almost constant thereafter. Apertures are deeply excavated with a small to

moderate acute angle between dorsal and apertural margins in profile. Most important, thecal spacing is low for a pendent species, remaining at 12 or 13 per 10 mm distally, the same as that in *D. 'protobifidus'*.

DISCUSSION. This species is probably a *D. 'protobifidus'* derivative in which thecal growth has continued in the distal part of the stipe. Similar thick species appear to have been derived on several occasions within the pendent didymograptid group. Of these only *D. diapason* has such low thecal spacing distally, and the thecae do not appear to become curved as width increases.

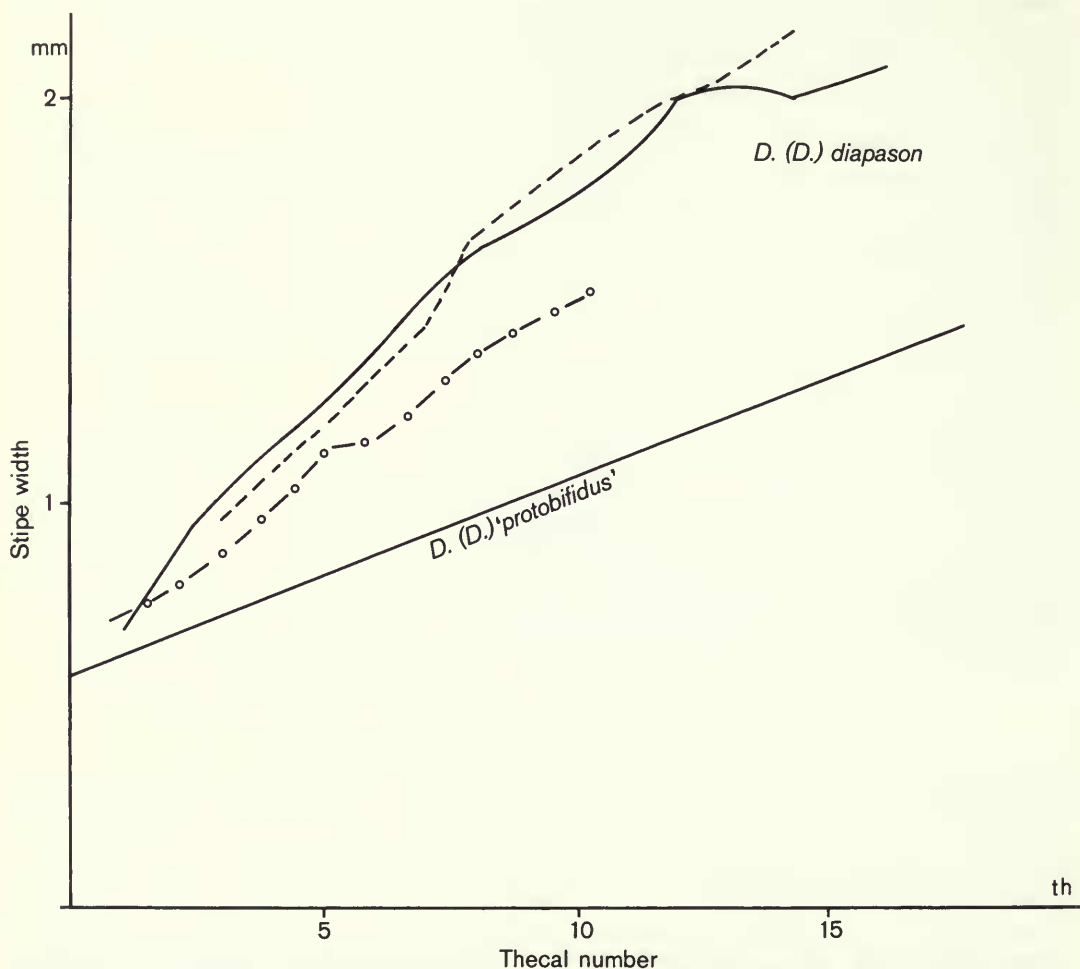


Fig. 38 Stipe expansion diagram for *Didymograptus (Didymograptellus) diapason* Chen & Xia. Median regression for *D. (D.) 'protobifidus'* shown for comparison.

Of other Arenig species with thick stipes *D. millardensis* Braithwaite (1976: 43–44; pl. 9, figs 24–26) has densely spaced thecae, as does its probable senior synonym *D. smithvillensis* Berry (1970: 67, 69; figs 1e, g, 2a, b); both are likely to be 'overgrown' forms of *D. bifidus*, *sensu stricto*, and as such slightly younger. The taxonomic recognition of these stout forms is probably justified as they seem to form discrete populations. However, it is now clear that broad, *murchisoni*-like species existed in the earlier part of the middle Arenig as well as in the Llanvirn.

Didymograptus (Didymograptellus) cf. exilis Ni in Mu *et al.* 1979

Fig. 39a–c; Pl. 5, figs 4, 5

cf. 1979 *Didymograptus exilis* Ni in Mu *et al.*: 58; pl. 19, figs 11, 12.

STRATIGRAPHIC RANGE. From one bed in the Olenidsletta Member, 49 m from base, V₁b, *D. protobifidus* Zone, associated with *Isograptus scandens* sp. nov. (p. 257).

MATERIAL. PMO NF3381–4, and several others.

DESCRIPTION. This small species lies outside the *bifidus*–‘*protobifidus*’ group to which the two species above belong. Isograptid development is interpreted from one specimen (Fig. 39b); this seems to be associated with the slightly lop-sided appearance of the proximal end, the squarer side being where the crossing canal comes over the back of th1¹ to initiate the second stipe. Hence we assign the species to the subgenus *Didymograptellus*. Sicula is 1.1 mm long, including a short nema 0.1 mm long, and its distal width is about 0.25 mm where it is prolonged into a lip forming a distinct, acute projection. Theca 1¹ originates very high on the sicula, almost certainly from the prosicula, attaining a length of 1.4 mm. Acute angles between the dorsal wall and apertural margins are typical of this, and all subsequent thecae. Theca 1² of similar character, but with its aperture about 1 mm along the opposing stipe. Maximum stipe curvature is at these first two thecae so that by the second thecal apertures on both stipes the stipes are virtually parallel and remain so thereafter. At the level of the first theca stipe width (dorsal margin to tip of thecal denticle) is only 0.5 mm. Stipe width increases slowly and slightly to a maximum of about 0.8 mm at th3, and is virtually constant thereafter to th8 (beyond which our specimens do not grow). Thecal inclination is constantly low (20°–25°), with corresponding low thecal overlap. Distance between apertural denticles on proximal thecae is large (about 0.75 mm), and the spacing becomes closer distally, down to as little as 0.5 mm, but the specimens are too small for spacing in 10 mm to be meaningful.

DISCUSSION. This species, with its slender stipes, low thecal inclination and small size is clearly different from the ‘*protobifidus*’ populations which are the commoner pendent populations at this horizon. While its general habit recalls such species as *D. nanus* Lapworth 1875, the sicula in that species is long and narrow (exceeding 2 mm in length) and th1¹ has an origin low on the metasicula, and as such is typical of the Llanvirn group of species for which the development is typified by *D. minutus*. It is unlikely to be closely related.

Ni (in Mu *et al.* 1979: 58; pl. 19, figs 11, 12) described the slender species *D. exilis* from a similar horizon to the Spitsbergen form in south-west China; like our species it shows conspicuous asymmetry at the proximal end, and is similar with regard to length of sicula and thecal

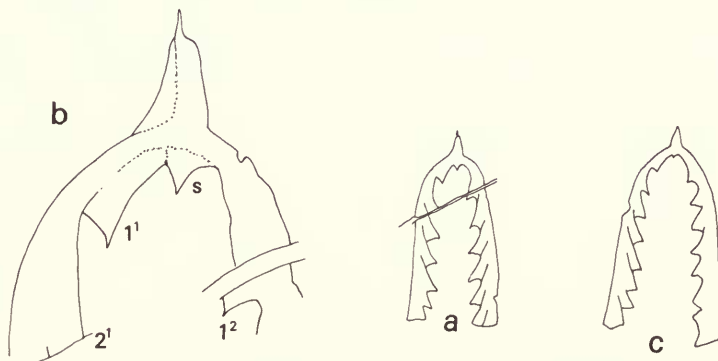


Fig. 39 *Didymograptus (Didymograptellus) cf. exilis* Ni. a, b, PMO NF3343, rhabdosome ($\times 3$) and enlargement of proximal end ($\times 12$), showing indication of isograptid arch, accounting for lop-sided appearance of flattened profile, and demonstrating *Didymograptellus* affinity. c, NF3344; $\times 3$. Both 50 m from base of Olenidsletta Member on Olenidsletta, in bed with *Isograptus scandens* sp. nov.

inclination. Ni's specimens are smaller, not growing beyond th3 or 4, and if anything the stipes are even narrower. Ni also mentions a supposed *artus* development in her text; as we have shown elsewhere, development types are especially difficult to discern on slender species without isolated material, and particularly in view of the similar asymmetrical appearance of *D. exilis* to our material, we consider it possible that the Chinese material may also have had isograptid development. However, we are bound to record our caution in identifying with the Chinese species, and the determination is accordingly tentative.

Monsen (1937) has described several slender *Didymograptus* species from the Arenig of Norway: *D. protoindentus* Monsen, *D. nanus* Lapworth, *D. minutus* Törnquist and a subspecies *pygmaeus* Monsen, and *D. protobifidus praecursor* Monsen. Of these the first and last named have stipes that diverge distally and have long siculae, exceeding 2 mm in length. The type specimen of *D. minutus* Törnquist (1890: pl. 1, figs 7, 8; see Bouček 1973: 78) is also from Arenig strata in Sweden, but unlike our species the sicula carries a long nema, and even without it is about 2 mm long. Monsen's subspecies *pygmaeus* is not well described, but if the stipe width quoted (0.3 mm) is correct this is far narrower than our material. The specimens attributed to *D. nanus* by Monsen differ from the Llanvirn type examples of that species in the same way as our material, mentioned above. Monsen (1937: pl. 2, fig. 38) clearly indicates a high sicular origin for th1¹, and her pl. 2, fig. 39 shows the arch formed by the crossing canals as typically seen in the isograptid development (see *D. bifidus* herein). Hence these '*nanus*' specimens are very like our specimens from Spitsbergen here attributed to *D. cf. exilis*; the sicula appears to be slightly more acute on Monsen's figures. Obviously it would be desirable to have more information on population variability in this case, and there are not enough specimens from Spitsbergen to provide it. But the probability is that the Chinese, Norwegian and Olenidsletta Member specimens belong to a single species.

Didymograptus (Didymograptellus) cf. meitanensis Chen in Mu *et al.* 1979

Fig. 35e

cf. 1979 *Didymograptus meitanensis* Chen in Mu *et al.*: 61; pl. 20, figs 7–9.

STRATIGRAPHIC RANGE. The earliest pendent didymograptid in the Spitsbergen succession, 17 m from base of the Olenidsletta Member, Lower Arenig (high Bendigonian).

MATERIAL. PMO NF2844, NF2849.

DISCUSSION. This early pendent species is similar to *D. 'protobifidus'* in most respects, but occurs stratigraphically below the abundant typical forms of that species, such as those shown on Pl. 2, fig. 1, and with a late Bendigonian fauna having *Tetragraptus (Pendeograptus) fruticosus* as a common associated species. This didymograptid has the lop-sided appearance of the proximal end that we associate with *Didymograptus (Didymograptellus)*. Like *D. 'protobifidus'* the thecal spacing is only 12–13 in 10 mm; stipes achieve a maximum width of about 1.3 mm. The main difference from *D. 'protobifidus'* resides in the higher degree of thecal overlap, so that the stipes lack the deeply indented appearance characteristic of *D. 'protobifidus'*. At about th10 *D. 'protobifidus'* typically has the thecal aperture cutting in to nearly half the total stipe width, whereas in *D. cf. meitanensis* that is only about a third. This may well represent the earliest stage of the '*protobifidus*'–*bifidus* population shift, but because of its early stratigraphic occurrence the form is recorded separately here. Mu *et al.* (1979) have named a large number of pendent species from about the same horizon as our species, but it is difficult to use the descriptions of the Chinese material for a critical determination of our specimens. *D. eobifidus* Chen & Xia (in Mu *et al.* 1979: 60–61; pl. 20, figs 1–6) is generally similar, but the quoted thecal spacing is denser (about 15 in 10 mm measured from their photographs). The closest species from the Chinese descriptions is probably *D. meitanensis* Chen, and we tentatively compare our material with that species. What is clear is that the Arenig pendent didymograptid radiation has produced a highly variable set of morphotypes (matching that in the Llanvirn); how many of these are 'real' species will depend on careful numerical analysis, and especially on the discovery of more material which can be isolated.

Didymograptus (Didymograptellus) multiplex sp. nov.

Pl. 1, figs 1–5

DIAGNOSIS. *Didymograptellus* species showing a transition from isograptid to *artus* development. Theca 2¹ typically aborted, not giving rise to a stipe series. Theca 1¹ dicalycal, development dextral. Habit slender, sicula about 1 mm long; stipe width at first theca only 0.5 mm, about 1.1 mm at sixth theca. Thecae with very low inclination, apertures deeply indented, flared, with prominent denticles.

STRATIGRAPHIC RANGE. High mid-part of the Olenidsletta Member (V₂a), the youngest pendent didymograptid in our section. 91 m from base, upper part of the Arenig *D. bifidus* Zone.

MATERIAL. **Holotype**, isolated proximal end, PMO NF3369. Other isolated specimens, PMO NF3370–3, are paratypes.

NAME. ‘Several-formed.’

DESCRIPTION. This species is based on isolated material, and its important characters relate to features which are probably only to be discerned on such material. However, it is such an important species for understanding the evolution of the astogeny of graptoloids, and its proximal end structure is so singular, as to justify the erection of yet another pendent didymograptid species.

Sicula short, 1.0–1.3 mm long, excluding nema, which we have seen up to 0.4 mm long. Sicular aperture 0.3–0.4 mm wide, with ventral lip up to 0.2 mm long. Theca 1¹ begins high on the sicula, 0.3 mm from its apex (excluding nema), presumably just below the base of the prosicula, and grows alongside the sicula for 0.6–0.75 mm, before swinging outwards and away from the sicula, making an acute angle with it. No more than 0.2 mm of the ventral side of the sicula is free from th1¹; the free, curved ventral wall of th1¹ extends to 0.8 mm, so that total length of first theca is about 1.4 mm; aperture oval with elongation in the sagittal plane, width 0.4 mm. Foramen for origin of th1² visible on dissected specimen (Pl. 1, fig. 1) at about halfway along proximal, downgrowing part of th1¹, crossing canal passing in front of sicula as a stout tube 0.2 mm in diameter, before curving down in the same fashion as th1¹, such that its eventual apertural position is slightly below that of th1¹ on the opposing stipe. Origin of th2¹ clearly seen on the holotype (Pl. 1, fig. 2) close to proximal end of th1², such that the ventral walls of the crossing canals form the characteristic arch typical of isograptid development. The width of th2¹ is only half that of th1². On the holotype th2¹ curves over on to the back of the first stipe as it would in normal isograptid development. However, at a length of only 0.5 mm this theca terminates with a tiny aperture scarcely more than 0.1 mm in diameter. The next theca on the first stipe originates not from th2¹ but from th1¹. This is clearly shown on the two best-preserved proximal ends, and is not a pathological development. Hence the proximal two apertures on the first stipe belong to th1¹ and th3¹, developmentally speaking. Subsequent growth is as usual in pendent didymograptids, although we have no stipes with more than six thecae. Stipe width at first theca only about 0.5 mm, increasing gradually to 1.1 mm at the fifth theca. Apertures are deeply excavated so that more than half of the thecal length lies free, and the angle between the free wall and aperture is a low acute angle distally. Centre tip of each aperture turned out into a short lip. If we take the distance between fifth and sixth thecae to indicate distal thecal spacing this would give 14 in 10 mm. It is probable that the stipes became virtually parallel at the second theca, but the sample is quite inadequate to determine any variation in this character.

DISCUSSION. The proximal end structure described above distinguishes this species from all other graptoloids. The species is unique in that it has two consecutive dicalycal thecae, and yet finishes up with only two stipes, one dichotomy (that producing th2¹) having aborted at an early stage. The ‘effective’ dicalycal theca is th1¹, yet the developmental type is initially isograptid; the species can thus be regarded as an intermediate stage in a transition between isograptid and *artus* development. Our two larger specimens (Pl. 1, figs 4, 5) are not as well

preserved as the proximal fragments, but neither shows any clear evidence of $th2^1$, and here development would no doubt be described as of *artus* type. Since all the specimens were recovered from a single small bed, and agree in all other characters, there is no reason to suppose that more than one species is represented. The larger specimens have either passed into *artus* development (i.e. completely suppressed the $th2^1$ dichotomy), or at a later stage the remnant $th2^1$ has been resorbed. We regard the species as particularly important in demonstrating the derivation of the *artus* type of development from the isograptid. Moreover it occurs at an appropriate geological horizon, because the pendent species occurring in earlier Arenig strata (where proximal structure is known from good material) have isograptid development, whereas the *artus* development is typical of Llanvirn species.

It would be difficult to recognize the new species without excellently-preserved material. According to Törnquist's original (1879) description of *D. minutus* the sicula of that species is 2 mm long, much longer than in our species. Specimens assigned to *D. minutus* by Bouček (1973) are not so different in sicular length, but the stipes remain consistently narrow; another of Bouček's species, *D. protobifidoides*, reaches a similar distal stipe width, but the thecae are not so deeply excavated, nor are they curved as in our species. Descriptions from flattened material are in general far too schematic to be useful in comparing with our form. Apart from the extra dichotomy, its proximal end structure is generally similar to that of *D. bifidus* (Hall), which underlies it in the Valhallfonna Formation, and it seems reasonable to regard *D. multiplex* as a late derivative of that species, one possibly lying at the root of subsequent pendent didymograptids (*Didymograptus*, *sensu stricto*).

Didymograptus (Didymograptellus) 'protobifidus' Elles 1933

Fig. 35a–d; Pl. 2, fig. 1

- 1933 *Didymograptus protobifidus* Elles: 98–99; text-fig. 1 (p. 110); *non* text-figs 2, 3.
- 1935 *Didymograptus protobifidus* Elles; Benson & Keble: 285–286, text-fig. 3.
- 1937 *Didymograptus protobifidus* Elles; Ripper: 154–156, text-figs 1, 2, 3, 8.
- non* 1937 *Didymograptus protobifidus* var. *praecursor* Mosen: 152–153; pl. 3, figs 18, 34; pl. 9, fig. 10; pl. 10, figs 13–15.
- 1944 *Didymograptus protobifidus* Elles; Decker (*pars*): pl. 52, fig. 9; pl. 53, fig. 9.
- ?1947 *Didymograptus protobifidus* Elles; Ruedemann: 343–344; pl. 54, fig. 18.
- 1960 *Didymograptus protobifidus* Elles; Berry: 63–64; pl. 8, figs 5–9.
- 1963 *Didymograptus protobifidus* Elles; Ross & Berry: 90; pl. 4, figs 6, 12.
- 1970 *Didymograptus protobifidus* Elles; Dewey, Rickards & Skevington: text-fig. 3m–p; fig. 4f–h.
- ?1973 *Didymograptus protobifidoides* Bouček: 80–81.
- 1976 *Didymograptus protobifidus* Elles; Fortey: 275–276, text-fig. 4a–c.
- 1977 *Didymograptus protobifidus* Elles; Carter & Churkin: 15; pl. 1, figs 5, 8.
- 1979 *Didymograptus protobifidus* Elles; Cooper: 71, text-figs 44a–e; pl. 10, figs d–f.
- ?*non* 1979 *Didymograptus protobifidus* Elles; Mu *et al.*: 58–59; pl. 19, figs 13–20.

STRATIGRAPHIC RANGE. ?25, 30–65 m from base in the Olenidsletta Member, below and intergrading with *D. bifidus* (Hall).

MATERIAL. Specimens additional to those given in Fortey (1976: 275–276) include PMO NF1846.

DISCUSSION. This species has been described in general terms by Fortey (1976: 275–276) and discrimination from *D. bifidus* has been given in the discussion of that species, and will not be repeated. Since there is perfect intergradation from '*protobifidus*' to *bifidus* passing upwards in the Spitsbergen succession there is no doubt that the earlier form merits taxonomic recognition, and, equally, that it must have had isograptid development and should be included within *Didymograptus (Didymograptellus)*. Morphologically homogeneous populations of *D. 'protobifidus'* cover whole bedding planes at about 60 m from the base of the Olenidsletta Member (Pl. 2, fig. 1).

The application of the name '*protobifidus*' needs some justification. The majority of the species given in the synonymy are genuine synonyms of the Spitsbergen form; what is less

certain is the identity of this group with the type specimen of *D. protobifidus* Elles from the Skiddaw Slates. Most of the specimens other than the type figured in Elles & Wood (1901) are not of the pendent *Didymograptus* group at all, but are poorly preserved specimens of *Aulograptus*, a feature also noticed independently by J. Riva & C. Jenkins (personal communication). Nor is the exact horizon of the holotype known, although Jackson (1964) records *D. cf. protobifidus* from the Arenig part of the Lake District succession. The type specimen, which occurs by itself in the type slab, is too poorly preserved to be sure whether the development is isograptid or not. On the other hand its general dimensions are close to those of the *protobifidus* from Spitsbergen; we see no evidence of tectonic distortion, and the rather coarse lithology in which the type occurs would argue against distortion of the specimen. The name is well established in the literature and it would be difficult to justify using any other name even though some of the critical details are missing from the type specimen. Hence we use the name here, but in quotes to denote our reservations about its true identity.

Extensiform didymograptids

Bouček & Přibyl (1951) proposed the genus *Expansograptus* based on *D. extensus* (Hall) to include extensiform didymograptids. It is clear that the gross rhabdosomal form is not a guide to the true phylogenetic relationships. Even within a species there is variation from horizontal to slightly declined or slightly reclined, and there is as yet too little evidence on proximal end structures to be certain that all generally extensiform didymograptids constitute a monophyletic group. No doubt this is the reason for Bulman (1970) taking the cautious approach of synonymizing *Expansograptus* with *Didymograptus*, *sensu lato*. We have begun to recognize what we believe are monophyletic groups within graptoloids of didymograptid grade of organization (see *Didymograptellus* above, and *Xiphograptus* below). The use of *Expansograptus* may be justified (although it is still not entirely satisfactory) for those didymograptids with isograptid development, sicula 1–2 mm long forming a relatively broad cone and usually distally curved, and a generally extensiform rhabdosome habit, although this may be with declined or slightly reclined proximal part. We exclude from *Expansograptus* those stout species which are markedly deflexed with the bend at about the 8th to 14th theca, such as *Didymograptus retroflexus* Perner (see Bouček 1973: pls 9, 10), for which the name *Corymbograptus* Obut & Sobolevskaya 1964 may be applicable. This usage of *Corymbograptus* cannot be extended to *all* deflexed species, however, as apparently advocated by Bouček (1973). Examination of populations of such slender deflexed species as *D. nitidus* shows that the amount of deflection at the proximal end varies, and that most characters of the sicula and thecae are like those of *Expansograptus*. This again demonstrates the difficulties of using gross rhabdosomal form as a *sine qua non* in the definition of genera.

Subgenus *EXPANSOGRAPTUS* Bouček & Přibyl, 1951

TYPE SPECIES. *Graptolithus extensus* Hall 1858.

REVISED DIAGNOSIS. Didymograptids with extensiform to slightly declined, deflexed or reflexed rhabdosome habit. Development of isograptid type and dextral mode. Sicula 1–2 mm long, not greatly elongate, lacking virgella, distally curved in the opposite direction to $th1^1$ so that its aperture is in line with those of stipe series. Theca 1^1 originating high on sicula; $th1^1$ and $th1^2$ enclosing an angle ranging from highly acute to almost 180° . Proximal stipe width exceeds 0.5 mm. Rate of expansion of stipes varies widely: may be slow and continuous, or relatively rapid near proximal end with no subsequent increase.

Didymograptus (Expansograptus) extensus (Hall 1858)

Fig. 40a–e; Pl. 6

1858 *Graptolithus extensus* Hall: 132.

1865 *Graptolithus extensus* Hall; Hall: 80–82; pl. 2, figs 11–16.

- non 1870 *Didymograptus extensus* (Hall) Nicholson: 341: pl. 7, figs 2, 2a.
 ?non 1875 *Didymograptus extensus* (Hall); Lapworth in Hopkinson & Lapworth: 642; pl. 33, figs 1a–d.
 1901 *Didymograptus extensus* (Hall); Törnquist: 14; pl. 1, figs 25–30.
 non 1901 *Didymograptus extensus* (Hall); Elles & Wood: 8–9; pl. 1, fig. 1.
 1904 *Didymograptus extensus* (Hall); Ruedemann (*pars*): 668; pl. 14, fig. 1.
 1937 *Didymograptus extensus* var. *linearis* Monsen: 115–116; pl. 1, figs 41, 47; pl. 7, figs 17, 20.
 1947 *Didymograptus extensus* (Hall); Ruedemann: 331–332.
 1960 *Didymograptus extensus* (Hall); Berry (*pars*): 60–61; pl. 8, fig. 10; non pl. 6, fig. 5.
 1963 *Didymograptus* aff. *D. novus* Berry; Ross & Berry: 89; pl. 4, fig. 8.
 1970 *Didymograptus extensus* (Hall); Dewey, Rickards & Skevington: 32.
 ?1973 *Expansograptus extensus* (Hall) Bouček (*pars*): 37–38, text-figs 10a, b; non figs 10c–f.
 1979 *Didymograptus extensus* (Hall); Cooper: 70; pl. 11b, e; text-fig. 42d.
 1979 *Didymograptus extensus linearis* Monsen; Mu *et al.* (*pars*): pl. 34, figs 1, 2; non pl. 33, figs 21, 22.

LECTOTYPE. Here designated **lectotype** is specimen no. GSC 976, original of Hall (1865: pl. 2, fig. 12), and refigured here as Fig. 40d. The associated fauna on the same slab includes *Dichograptus octobrachiatus*, *Sigmagraptus praecursor* and *Phyllograptus ilicifolius*, and some very wide, apparently extensiform graptolite fragments. This assemblage would suggest a horizon in the earlier middle part of the Arenig, above the *T. approximatus* Zone, and possibly also that of *T. fruticosus*.

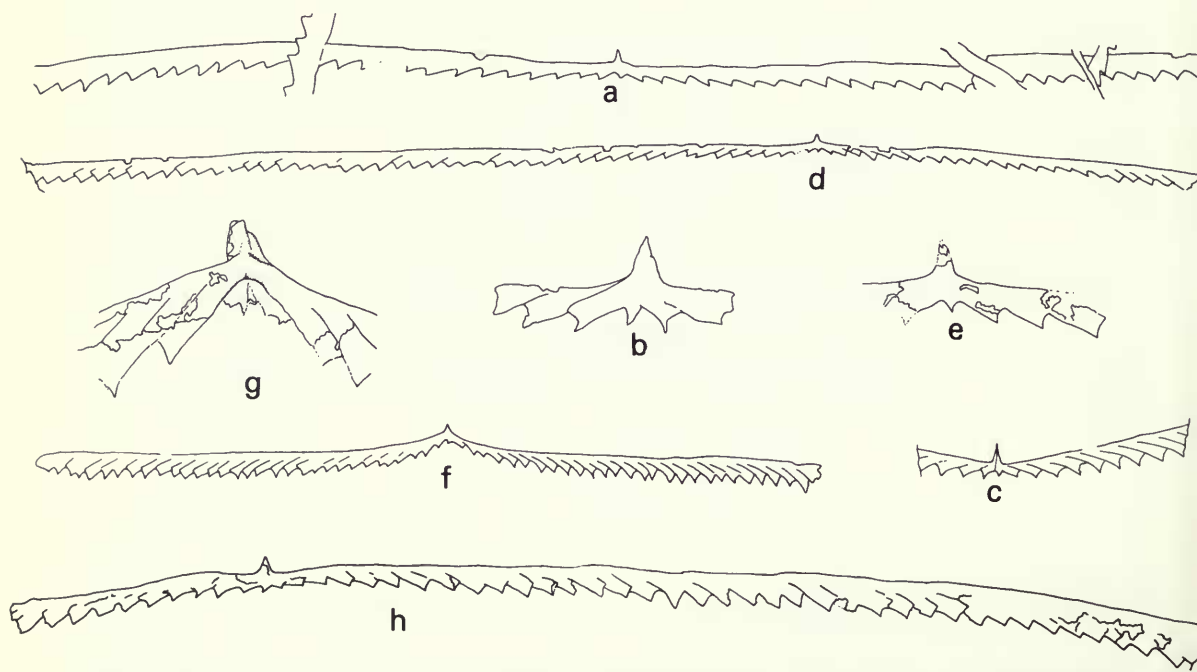


Fig. 40a–e *Didymograptus* (*Expansograptus*) *extensus* (Hall). a, SM A105813, part of very large but otherwise typical specimen from slab figured in Plate 5; lower part of Olenidsletta Member in Olenidsletta, 13 m from base; $\times 3$. b, growth stage from same slab as lectotype; $\times 6$. c, PMO NF2535, specimen preserved in relief with distinctly reclined stipes, $\times 3$. d, e, GSC 976, **lectotype** $\times 3$, and enlargement, $\times 6$, of proximal region showing curvature of thecae. Specimen figured by Hall (1865: pl. 2, fig. 12).

Fig. 40f, g *Didymograptus* (*Expansograptus*) *nitidus* (Hall). f, GSC 914e, rhabdosome from type series, showing general form; $\times 3$. g, GSC 914d, detail of proximal region preserved in relief, type series, showing isograptid arch and isograptid development type; $\times 8$.

Fig. 40h *Didymograptus* (*Expansograptus*) *ensjoensis* Monsen. PMO NF3347, lowest part of Olenidsletta Member, not more than 6 m from base, southern melt stream; $\times 3$.

STRATIGRAPHIC RANGE. Lower part of Olenidsletta Member, V₁b, 2 to 75 m from base, corresponding to the upper part of the Bendigonian (three-branched *fruticosus* interval) and the overlying *D. 'protobifidus'* Zone.

MATERIAL. SM A109727 (many specimens); PMO NF1764, NF2813.

DESCRIPTION. Both the lectotype and the populations of *D. extensus* from Spitsbergen are very straight extensiforms; there is hardly any hint of declination at the proximal end. We have found only three specimens among Hall's type slabs, and all have this habit, and it is consistent in the larger populations from Spitsbergen; hence we regard this as an important character in taking a strict view of *D. extensus*. The sicula is short, 1.5–1.6 mm long, curved distally, probably with a short lip, so that the aperture lines up with that of th1². Theca 1¹ probably had a high origin on the sicula, and distally extends to a point well below the sicular aperture: th1² is of similar form, the free walls between th1¹ and th1² making an angle of 110°–130°, the point of the sicular profile more or less bisecting this angle. Development isograptid. The stipe expansion diagram (Fig. 41) shows a gradual and continuous increase in

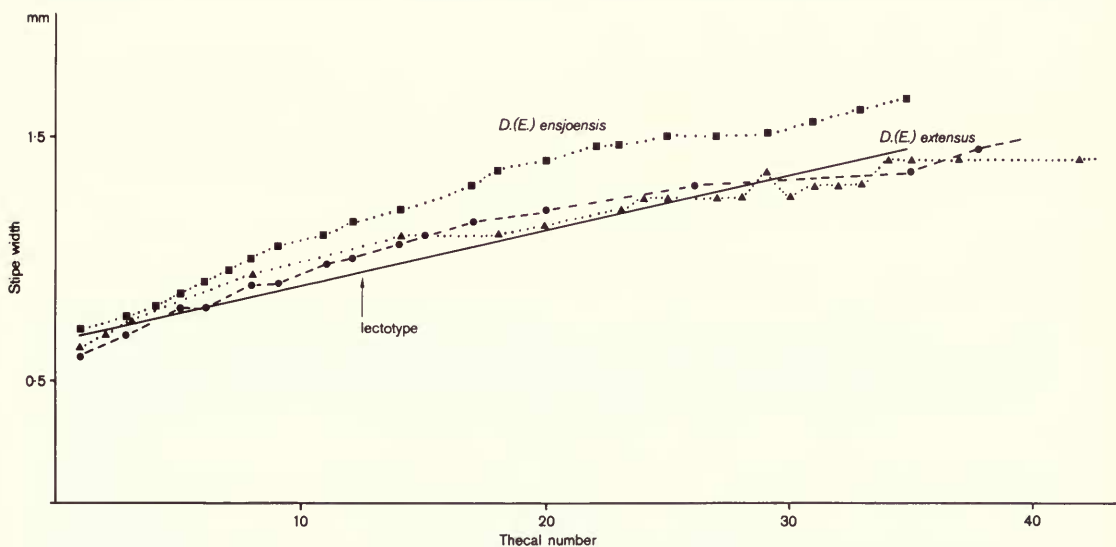


Fig. 41 Stipe expansion diagrams for *Didymograptus (Expansograptus) extensus* and *D. (E.) ensjoensis*. Line is calculated regression from the lectotype of *D. (E.) extensus*.

width of stipes which is quite characteristic. At the proximal end the stipes are always less than 0.8 mm width measured to the apertural denticles: 0.7 mm is typical. The stipes appear to have continued growing to a great length. Some of the fragmentary stipes on Hall's type slabs are 2 mm broad, and since the longest stipes in contact with the proximal end are only 1.6 mm broad, and this is at th60, it seems probable that individual stipes exceed 20 cm and may have approached 30 cm in length. Proximal thecal inclination is low, 20°–25°, and about 30° distally, with the proportionate amount of thecal overlap increasing in the usual way. Judged from the form they adopt when compressed it is likely that the ventral walls of the distal thecae were embraced by the dorsal walls of the preceding thecae. An important character is that the angle between the free ventral wall of the thecae and its aperture is approximately a right angle; in many other extensiform species this angle is acute. Distance between the apertures of th1¹ and th1² is slightly less than 2 mm. Thecal spacing is in general rather low, 8–9 thecae in 10 mm in the distal part of the stipe. Thecae were probably minutely denticulate.

DISCUSSION. Populations from low in the Olenidsletta Member agree exactly in their proportions and proximal end thecal characters with the lectotype (Fig. 40d). Törnquist (1901: 15) pointed out that the specimens used by Elles & Wood (1901) from the English Lake District

to describe *D. extensus* differed both from Hall's types and from Scandinavian specimens in having a distinctly declined proximal portion, after the manner of *D. nitidus*. The immediately straight stipes of *D. extensus* appear to be a consistent character, typifying populations covering large bedding planes in Spitsbergen. The British forms have therefore to be excluded from *D. extensus* (Hall). Bouček's (1973) concept of *D. extensus* seems to be based on the British material, at least as far as his pl. 6, fig. 5 is concerned; however, his text-figs 10a, b appear to have straighter proximal parts, but even here the angle between the free ventral walls of $th1^1$ and $th1^2$ appears to be acute, and unlike the type *D. extensus* in this regard. It seems possible that true *D. (Expansograptus) extensus* was absent from the boreal realm during the Arenig.

We have taken a narrow view of *D. extensus* here, that is, we have only identified those specimens which compare closely with the lectotype. As thus constituted the species seems to be confined to the earlier half of the Arenig. Berry (1960) records it as early as the *T. approximatus* Zone, although his figured specimen (1960: pl. 6, fig. 5) shows reclined stipes and apparently acute thecae and is probably not referable here. However, *D. extensus* is certainly characteristic of the *T. fruticosus* and *D. protobifidus* Zones over a wide area of the Pacific Province; Thomas (1960) records it throughout the Bendigonian and Chewtonian of Australia, and Cooper (1979) records a similar range in New Zealand.

Didymograptus (Expansograptus) ensjoensis Monsen 1937

Fig. 40h

STRATIGRAPHIC RANGE. Lowest part of Olenidsletta Member, not more than 6 m from base, V_1a , early Arenig (*T. fruticosus* Zone).

MATERIAL. PMO NF3347 (several specimens).

DESCRIPTION. *D. ensjoensis* has been rather widely recorded from the earlier part of the Arenig. Monsen's original description gives two photographs and a line drawing; her pl. 7, fig. 12 shows the slightly reflexed profile to either side of the sicula which is displayed on our well-preserved specimen. As Monsen points out, the proximal end structure is much like that of *D. extensus*, and in terms of stipe expansion (Fig. 41) the species is distinguished only by its steeper gradient, representing an earlier attainment of a greater stipe width. The stipe eventually stabilizes in width at about $th20-30$. Monsen mentions a maximum width of 2.2 mm; in fragmentary distal stipes associated with our specimen with a proximal end, stipes up to 2 mm broad occur. Distal thecal spacing is 9–10 in 10 mm.

As in *D. extensus* the sicula is relatively short, 1.6 mm, in comparison with the eventual stipe width; it is curved away from $th1^1$. Monsen describes a high origin for $th1^1$, but our material is too heavily carbonized to be sure of this feature. Theca 1^1 and $th1^2$ diverge at a high obtuse angle, with the distal part of the sicula hanging down as a small 'tooth' between – a feature well shown also in Monsen's (1937) pl. 7, fig. 14. Width of stipe at the level of the first thecae is 0.70–0.75 mm. Thecal inclination is initially low (about 20°), with correspondingly low thecal overlap. In the distal part of the stipe the preservation suggests that the thecae had by then become very broad tubes, resulting in their imbrication on flattening. As in *D. extensus* the angle between the free ventral wall and the thecal aperture is rarely acute, and usually about a right angle.

DISCUSSION. Harris & Thomas (1940) record *D. ensjoensis* from the Bendigonian of Australia; the proximal end they figure (1940: pl. 2, fig. 15B) compares with our material, although the distal stipe width is said to be 2.5 mm, which is greater than on our material or on the type. Distal thecal spacing is given as 8 in 10 mm, which is a little wider than in the specimens from Spitsbergen. A more closely comparable specimen is figured by Cooper (1979: pl. 11a) from the Bendigonian of New Zealand. Mu *et al.* (1979: 107) record a rather strongly reclined specimen from their zone of *Didymograptus filiformis* in south-west China.

D. similis (Hall 1865) may be confused with this species. The stipe expansion diagram (Fig. 42), incorporating the two of Hall's specimens with proximal ends preserved, shows that *D.*

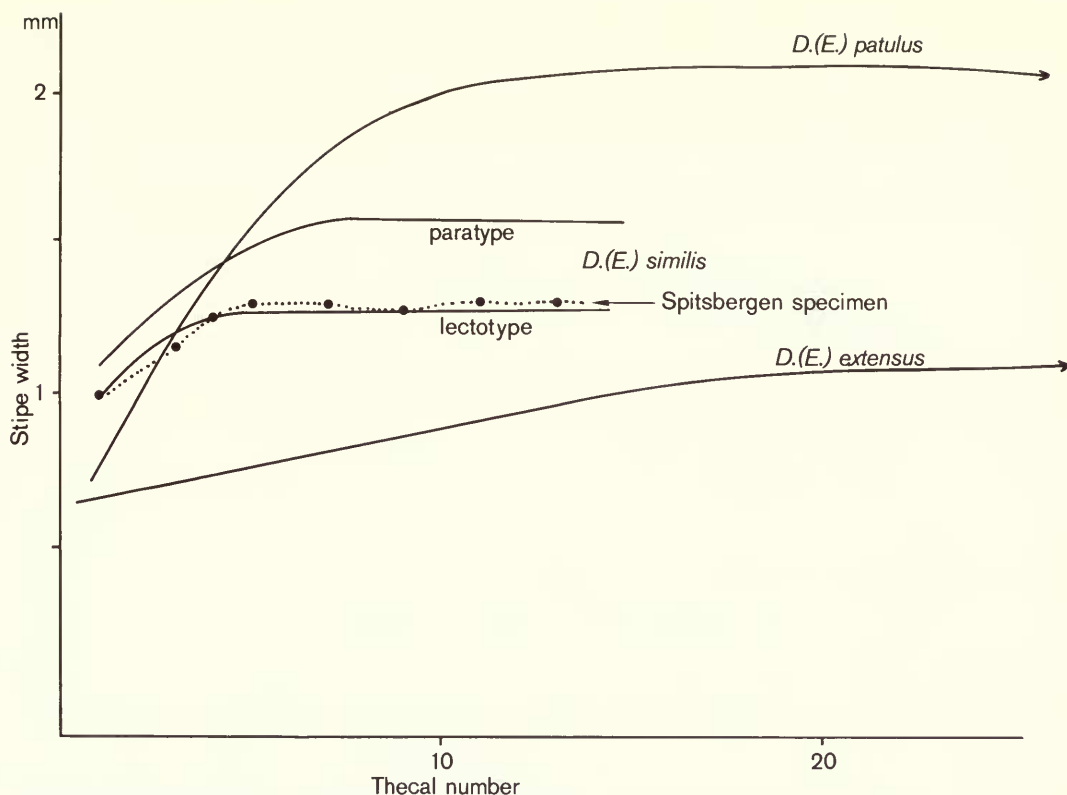


Fig. 42 Stipe expansion diagrams for the extensiform *Didymograptus* (*Expansograptus*) types of Hall (1865) relevant to the species found in Spitsbergen. Curves fitted by eye. Two type specimens of *similis* give some spread of variation but are of similar growth form; Spitsbergen example shown.

similis has wider stipes proximally, and soon reaches its maximum width, a shape unlike that of *D. ensjoensis*.

Didymograptus (*Expansograptus*) *praenuntius* Törnquist 1901

Fig. 43a, b; Pl. 4, fig. 12

1901 *Didymograptus praenuntius* Törnquist: 17; pl. 2, figs 7–12.

?1937 *Didymograptus praenuntius* Törnquist; Monsen: 118–119; pl. 1, figs 27, 29.

1938 *Didymograptus asperus* Harris & Thomas: 76–78; pl. 2, figs 25a–c; pl. 4, fig. 23.

STRATIGRAPHIC RANGE. One bed low in the Profilbekken Member, 6 m from base, V₁a, early Arenig (Bendigonian).

MATERIAL. PMO NF475, NF495.

DESCRIPTION. This species has to be discussed in relation to *D. patulus* (Hall), which, as Törnquist (1901) noted, it closely resembles. Only one specimen is suitable to be selected as **lectotype** for *D. patulus*, the original of Hall (1865: pl. 1, fig. 10), GSC 918a, which unfortunately has lost the tip of the sicula. This is shown on Fig. 43c. Hall's type series includes a number of distal stipes, from which some idea of the variability of the species can be obtained. The characteristic features of *D. patulus* include especially the strongly curved thecal form, and the acute 'cut away' appearance of the thecal apertures, so that the free ventral walls of the thecae subtend an acute angle (30°–40°) with the concave apertural margins. The stipe expansion is also highly characteristic, with rapid expansion in thecal length and stipe width

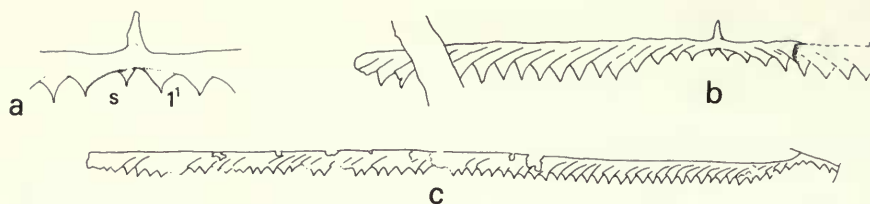


Fig. 43a, b *Didymograptus (Expansograptus) praenuntius* Törnquist. PMO NF475, rhabdosome in full relief, $\times 3$, and enlargement of proximal region, $\times 6$, showing isograptid arch and isograptid development; reverse views. Lowest part of Olenidsletta Member, V₁a, type section.

Fig. 43c *Didymograptus (Expansograptus) patulus* (Hall). GSC 918a, **Lectotype**, selected herein; the best preserved of Hall's (1865) original series, the original of his pl. 1, fig. 10; $\times 1.5$.

over the first 6 or so thecae, after which the stipe stabilizes at its maximum width. The specimens here attributed to *D. praenuntius* are similar to *D. patulus* in all these respects, and the stipe expansion has an exactly similar shape (Fig. 44). However, the maximum thickness achieved by the stipes is only about 1.5 mm, and all the stipe fragments in our population are in the range 1.4–1.6 mm. Hall's type series has the range 2.1 to 2.4 mm for stipe width; this variation is accounted for by continued thecal growth, for the apertural profiles are similar in all specimens, and the distance between the dorsal stipe margin and the addorsal margin of the apertures varies between 1.5 and 1.7 mm. The same dimension in our specimens lies between 0.9 and 1.1 mm. Törnquist (1901) characterized *D. praenuntius* as having the same form as *D. patulus* but with narrower stipes, and this seems to afford good grounds for our determination. It should be noted that our specimens are in full relief, and it is possible that if flattened the stipes would have become a little wider. Distal thecal spacing on the *D. patulus* type series is 9–11 in 10 mm, and is 9–10 in 10 mm in our population of *D. praenuntius*. The proximal end of one specimen is particularly well preserved (Fig. 43a). The sicula is 1.35 mm long (without preserved nema) and distally curves away from th1¹ in the way we have described as typical of the subgenus *Expansograptus*, so that its aperture is essentially in line with the thecae of the stipe². Theca 1¹ commences high on the sicula, and is longer, reflected in the greater length of its free ventral wall. Our specimen is in reverse aspect, and well displays the broad (0.3 mm) crossing canal connecting th1² and th2¹, showing isograptid development. The angle enclosed between the free ventral wall of th1¹ and th1² is about 115°. Thecal apertures are flared, like so many small trumpets, and have a small denticle.

DISCUSSION. Tjernvik (1960) records the range of *D. praenuntius* in the Flagebro drill core from the top of the zone of *Didymograptus balticus* through that of *Phyllograptus densus* to the base of the *Phyllograptus angustifolius elongatus* Zone. This range overlaps that of *Tetragraptus fruticosus*, and it is reasonable to suppose that the Scandinavian occurrences are of the same age as that in Spitsbergen. Monsen's (1937: 118–119) records from Norway may be of the same species, but the stipe widths recorded (1–1.3 mm) are rather narrow. Harris & Thomas (1938) described *D. asperus* from Australia and their description matches that given above for *D. praenuntius* very closely, although their figures are not adequate for satisfactory comparison. Thomas (1960) gives the range of this species as through all except the uppermost Bendigonian, which would accord with the horizon in Spitsbergen. The exact age of Hall's type population of *D. patulus* cannot be determined from associations on the type slabs. Raymond (1914) suggests that it occurs in Zone A at Levis associated with a *T. fruticosus* or *T. approximatus* fauna, which is in general accordance with Berry's (1960) record of *D. patulus* from the *T. fruticosus* and *D. protobifidus* Zones in the Marathon region, Texas. It seems to be an earlier Arenig species, like *D. praenuntius*. Törnquist's (1901) record of *D. patulus* from Sweden at a younger horizon is a misidentification: Chen (*in* Mu *et al.* 1979) has renamed this species *D. patulentis*. If Törnquist's observation (1901: 16) that there was a virgella on his material is correct this species should be referred to *Xiphograptus* gen. nov. (p. 289).

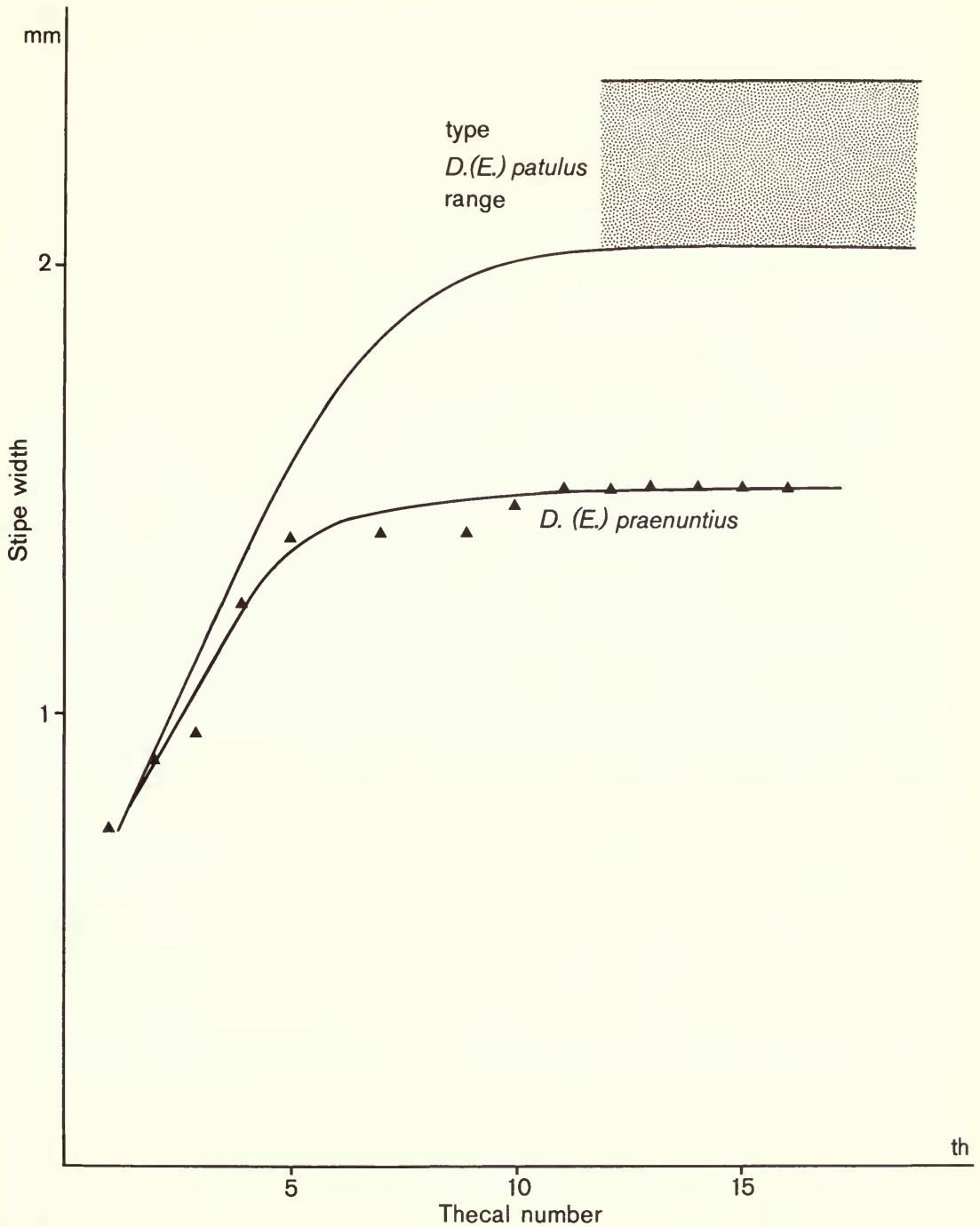


Fig. 44 Stipe expansion diagram for *Didymograptus (Expansograptus) patulus* (Hall) and *D. (E.) praenuntius* Törnquist. Stippled area shows spread of mature stipe widths associated with the type specimen of *D. (E.) patulus* in Hall's collection. Triangles plot best stipe from Spitsbergen.

Didymograptus (Expansograptus) similis (Hall 1865)

Fig. 45a-c

- 1865 *Graptolithus similis* Hall: 78-79; pl. 2, figs 1-5.
 non 1938 *Didymograptus similis* (J. Hall) Harris & Thomas: 76; pl. 2, figs 22a, b; pl. 4, fig. 20.
 1979 *Didymograptus constrictus* (J. Hall); Cooper (*pars*): fig. 42b; pl. 11, fig. f; *non* fig. 42a; pl. 11, fig. d (*constructus* spelling error on plate).

STRATIGRAPHIC RANGE. 17 m from base of Olenidsletta Member, early Arenig, V₁b (latest Bendigonian).

LECTOTYPE. The slab which contains the original of Hall's (1865) pl. 2, figs 2, 3 has on it two specimens of *D. (E.) similis*, one of which is judged to be the original of Hall (GSC 944b) and is here designated **lectotype**. This specimen is not in very good condition, particularly on the ventral side of the proximal end. On the same slab there are specimens of *D. (E.) extensus* and *Tetragraptus serra*, both of which are revised in this paper, and which occur with *D. similis* in Spitsbergen also.

MATERIAL. PMO NF2076.

DESCRIPTION. Rhabdosome horizontal, but with a characteristic gentle convexity to the dorsal stipe margin produced by a slight tendency to reclamation on either side of the sicula. Stipes grow to length of about 2 cm. Hall's (1865) pl. 2, fig. 3 shows an apparent arch at the proximal end with no sign of ventral protrusion of the sicula; this was probably a result of the rather poor preservation of the lectotype. The distal part of the sicula protrudes as a small 'tooth' between *th1*¹ and *th1*², but is very inconspicuous (about 0.25 mm long) rather in the manner of *D. extensus*. Total sicula length is 1.5-1.7 mm, and dorsally it forms a broad cone with the proximal part of *th1*¹, which must have had a high origin. Growth pattern differs from that of *D. extensus* (Fig. 42): the proximal stipe width at *th1*¹ is 1-1.2 mm, and there is only a slight increase in stipe width over the first 4 or 5 thecae to a maximum width of 1.25-1.55 mm which remains constant thereafter. Free ventral walls of *th1*¹ and *th1*² enclose an angle of 110°-130° and are about 1 mm long; the free walls of subsequent thecae are the same length (up to 1.2 mm), with thecae overlapping for about half their length. Thecal inclination is about 25° distally. Angle between ventral wall and apertural margin is usually somewhat acute. At the distal part of the stipe thecal spacing is 9 in 10 mm.

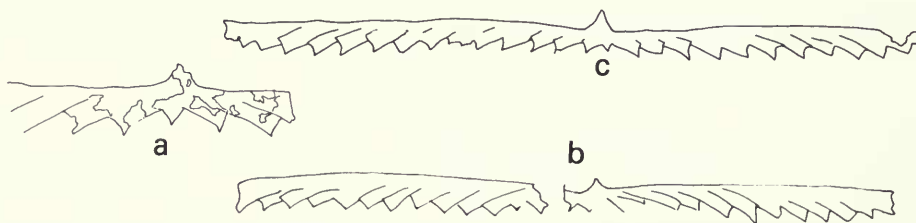


Fig. 45 *Didymograptus (Expansograptus) similis* (Hall). a, b, lectotype, GSC 944, proximal region ($\times 6$) and rhabdosome ($\times 3$). c, PMO NF2076, 18 m from base of Olenidsletta Member on Olenidsletta; $\times 3$.

DISCUSSION. Our Spitsbergen specimen compares exactly with the type material. The pattern of growth clearly distinguishes *D. (Expansograptus) similis* from *D. (E.) extensus* which it resembles in proximal end structure. It is very like *D. constrictus* (Hall), which differs significantly only in having the stipe width at *th1*¹ and *th1*² as wide as 1.7 mm, and attaining a width of 2 mm or more distally. *D. constrictus* appears to be typical of a somewhat earlier horizon (Zone A at Levis) than *D. similis*, and may, of course, intergrade with it stratigraphically. Figures of other North American material of *D. similis* are not good enough to be certain of their identity, although a manuscript note by O. M. B. Bulman records specimens which he states are identical with the types from Bed 2 at Deepkill. Berry (1960) identifies the species

from the top of the Bendigonian (three-branched *fruticosus*) through to the Arenig zone of *D. bifidus*, but without figuring specimens. The Australian specimens attributed to *D. similis* by Harris & Thomas (1938) are too narrow proximally and too wide distally to belong to this species. Of the specimens from New Zealand assigned to *D. constrictus* by Cooper one (1979: pl. 11, fig. f) has the proportions of *D. similis*; this is from the *D. protobifidus* Zone. A contemporaneous group of Scandinavian species centred on *D. suecicus* Tullberg 1880 may well prove to be close to *D. similis*, but the revision of these species is beyond the scope of this paper.

Subgenus *CORYMBOGRAPTUS* Obut & Sobolevskaya, 1964

TYPE SPECIES. *Didymograptus v-fractus* Salter 1863.

DISCUSSION. This subgenus is used with many reservations. As originally proposed by Obut & Sobolevskaya (1964) it was simply an upgrading of the old informal division by Elles & Wood of 'deflexed didymograpti'. There is no proof that the deflexed species constitute a monophyletic group, nor is our material from Spitsbergen sufficiently well preserved to decide whether there are any characters of the proximal end of the type species which might define a natural group. There is evidence to suggest that the deflexed species were produced by several 'bursts' at different times. In the European Arenig the abundant deflexed forms (*Didymograptus v-fractus*, *D. uniformis*, *D. vacillans*, *D. v-similis* and *D. deflexus*) are generally present low in the series, as they are in our successions in Spitsbergen and in Scandinavia. In south-west China (Mu *et al.* 1979) a whole range of deflexed species (purportedly 24 species) occurs along with the Arenig pendent *Didymograptus* (*Didymograptellus*) radiation and true *Phyllograptus* (as restricted in this paper), which indicates a mid-Arenig age, and there is no reason to suppose that this group of species is related to the earlier ones from Europe. In the later part of the Arenig (*D. hirundo* Zone and Castlemainian-Yapeenian) deflexed species are generally scarce, but one species which is very widespread in the Pacific Province is *Didymograptus v-deflexus* Harris (1924; see also *Corymbograptus v-fragosus* Obut & Sobolevskaya 1964), a gracile species with a short sicula which may be unrelated to any of the earlier forms. Finally, in the Llanvirn of Bohemia Bouček (1973) has described a series of robust species (*C. retroflexus* Perner 1895 and various subspecies, together with *C. imminutus*); if Bouček's (1973: 54) attribution of *artus* development to these is correct then it is probable that this group is more closely related to the Llanvirn pendent species *Didymograptus* (*Didymograptus*) than to earlier deflexed species.

Furthermore there are several species, *D. nitidus* Hall being one, in which the degree of deflection varies within wide limits. The variation extends from forms with marked change in direction of stipe growth, through those weakly declined, to those in which a gentle bend occurs at the sixth or seventh theca. Bouček (1973) assigns *D. nitidus* to *Expansograptus*, as he does *Didymograptus simulans* Elles & Wood 1901, even though both would fit his definition of *Corymbograptus*: 'stipes at first pendent, later, at some distance from the sicula, flexing sideward at an obtuse to straight angle' (1973: 49). It is obvious that a 'genus' which may have had as many as four separate origins, and into which the placing of certain species is almost impossible to decide, is scarcely a useful taxonomic category at the moment. Our use of it here is based on the type species, and the early Arenig deflexed group.

Didymograptus (*Corymbograptus*) *v-fractus* Salter 1863

Fig. 46c; Pl. 2, fig. 5

STRATIGRAPHIC RANGE. Lower part of Olenidsletta Member, 13–20 m above base, V₁b, early Arenig (late Bendigonian).

MATERIAL. PMO NF3364.

DISCUSSION. The one specimen is not well preserved, but it is of importance in providing a link with the earlier Arenig succession of the English Lake District. Distal thecal spacing is 10 in

10 mm, at the upper limit of the range given by Elles & Wood (1901: 34). Our stipes do not greatly exceed 3 cm in length; the specimens used by Elles & Wood to illustrate the species have a stipe width of 2 mm or slightly more at this length, which is the same as on our specimen. Examples with generally similar form have been figured by Monsen (1937: pl. 10, figs 6, 7), from the zone of *Phyllograptus densus* in Norway. The maximum abundance of deflexed didymograptids in the Lake District is in the earlier half of the Arenig series, and according to Jackson (1962) the stouter species, compared by him with *D. v-fractus*, are confined to the earliest zone, that of *D. deflexus*.

Didymograptus (Corymbograptus) cf. deflexus Elles & Wood 1901

Fig. 46a, b

STRATIGRAPHIC RANGE. Olenidsletta Member, 6–21 m from base, V₁b, early Arenig (late Bendigonian).

MATERIAL. PMO NF2395a, NF2804.

DISCUSSION. Several deflexed specimens from the earlier part of the Olenidsletta Member are included here. They are more slender than *D. v-fractus*, and with 13 thecae in 10 mm distally. Elles & Wood's (1901: 36) description of *D. deflexus* implies that the distal stipe width of their species was only 1 mm (ours are 1.3–1.4 mm); hence our identification is qualified. However, it is possible to find specimens from the Lake District (for example BM(NH) no. P.7159) with identical distal stipe width and thecal spacing to those of our specimens, and it seems probable that there is more variation in *D. deflexus* than Elles & Wood allowed. *Didymograptus cf. deflexus* of Monsen (1937: 146) is also very close to our material.

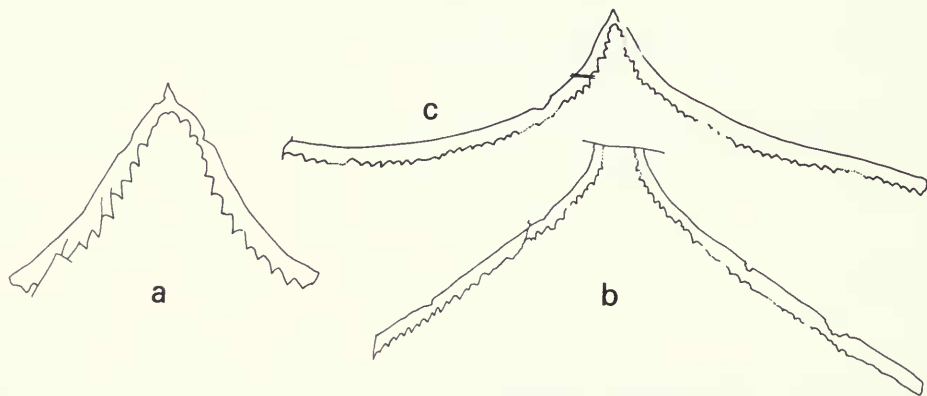


Fig. 46a, b *Didymograptus (Corymbograptus) cf. deflexus* Elles & Wood. a, PMO NF2395a, proximal part of rhabdosome; $\times 6$. b, PMO NF2804, poorly preserved incomplete specimen, showing characteristic distal declination of stipes; $\times 2$. 6 m from base of Olenidsletta Member on Olenidsletta.

Fig. 46c *D. (C.) v-fractus* Salter, PMO NF3364, 13–20 m above base of Olenidsletta Member, Olenidsletta; $\times 2$.

Didymograptus (sensu lato), cf. D. pennatulus Hall 1865

Pl. 4, fig. 9

STRATIGRAPHIC RANGE. Upper part of Olenidsletta Member 140 m above base, V₃, late Arenig, *Isograptus victoriae victoriae* Zone.

MATERIAL. PMO NF3377–8.

DISCUSSION. This very broad species occurs in one bed high in the Olenidsletta Member. It is preserved in full relief. We know it was an extensiform didymograptid, because a very poor proximal end which could not be collected was observed in the field. Maximum stipe width was

evidently attained rapidly and maintained over long distances (greater than 8 cm). The widest specimen is over 6 mm broad; thecae are long and curved, the apertural margin being almost parallel to the dorsal stipe wall. There are long apertural denticles. In a narrower specimen, 4.5 mm broad, the distal curvature of the thecae is not completed, and the apertures are still oblique, indicating that there was variation within the population in the ultimate width of the stipes. Specimens resembling the narrower one have been referred to as *D. hirundo*. The best comparison is with Hall's (1865) species *D. pennatulus*, which has similar stipe widths, according to Ruedemann (1947). However, forms which have been attributed to *D. pennatulus* apparently have a very long stratigraphical range, from the earlier part of the Arenig probably into the Llanvirn, and we doubt that all records represent the one species. Since the pendent didymograptids evidently produced massive 'overgrown' species on several occasions, we see no reason why this should not apply to extensiform species as well. Our determination is accordingly tentative.

Genus *PSEUDOPHYLLOGRAPTUS* nov.

TYPE SPECIES. *Phyllograptus angustifolius angustifolius* Hall 1858.

DIAGNOSIS. Quadriserial, scandent rhabdosome with four stipes united along their dorsal margins; median septa separating adjacent thecal series cruciform, imperforate; proximal development isograptid, dextral; initial thecae distally declined or horizontal, sicula lacks virgella.

NAME. Referring to the superficial similarity between the new genus and *Phyllograptus*, *sensu stricto*.

DISCUSSION. Dichograptids with phyllograptoid rhabdosomes in which the median septa are complete (imperforate) and more or less cruciform in cross section are here transferred to the new genus *Pseudophyllograptus*, with *Phyllograptus angustifolius angustifolius* as type species. The type material of *P. a. angustifolius* is redescribed here but the diagnostic characters of the genus are revealed only by relief material such as that from Sweden (*P. a. angustifolius*; Holm 1895) and Spitsbergen (*P. angustifolius chors* subsp. nov., p. 244). Isograptid development was inferred from a series of serial sections of the Swedish form by Bulman (1936a), and is also inferred from serial sections for the material from Spitsbergen described here, where overall development of the rhabdosome follows the *T. bigsbyi* plan.

Where the internal rhabdosome structure is unknown, the following may prove useful in distinguishing the genus from *Phyllograptus*. The distal portions of the first pair of thecae, 1¹ and 1², are pendent or horizontal rather than growing upwards as in *Phyllograptus*, and they lie in the interangle between the two stipes on each side rather than forming part of the second-order stipes themselves, as in *Phyllograptus typus*: see p. 280. The rhabdosome has a more rounded proximal end and a more nearly parallel-sided outline; thecae throughout the rhabdosome have a higher initial angle of inclination to the long axis of the rhabdosome and

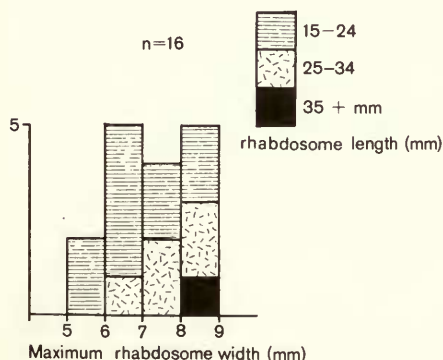


Fig. 47 *Pseudophyllograptus angustifolius angustifolius* (Hall), type population; frequency distribution of rhabdosome width (taken to nearest whole number). Rhabdosome length shown by pattern; note that longer rhabdosomes have greatest width.

are less curved, especially in the proximal part of the rhabdosome. Even if only fragmentary three-dimensional material is available a transverse section of the axial region should reveal the cruciform median septum.

SPECIES AND SUBSPECIES. *Phyllograptus angustifolius* Hall 1858, *P. a. elongatus* Bulman 1931, *Pseudophyllograptus angustifolius chors* subsp. nov., *Pseudophyllograptus angustifolius* subsp. 1, *Phyllograptus densus* Törnquist 1879, and *P. typus* var. *parallelus* Bulman 1931.

In addition to *Pseudophyllograptus angustifolius chors* and the nominate subspecies, diagnostic rhabdosome structure is also present in a specimen here attributed to *Phyllograptus densus* Törnquist from Kinnekulle, held by the New Zealand Geological Survey, and preserved in partial relief. *P. typus* var. *parallelus* Bulman 1931 and *P. angustifolius elongatus* Bulman 1931 are included on grounds of their relatively straight and highly inclined thecae, particularly in the proximal part, combined with an approximately parallel-sided rhabdosome. Judged from their published photographs, several of the phyllograptoids described by Mu *et al.* (1979) are likely to belong to *Pseudophyllograptus*.

Pseudophyllograptus angustifolius angustifolius (Hall 1858)

Fig. 48e, f

1858 *Phyllograptus angustifolius* J. Hall: 139.

1865 *Phyllograptus angustifolius* Hall; J. Hall: 125; pl. 16, figs 17–21.

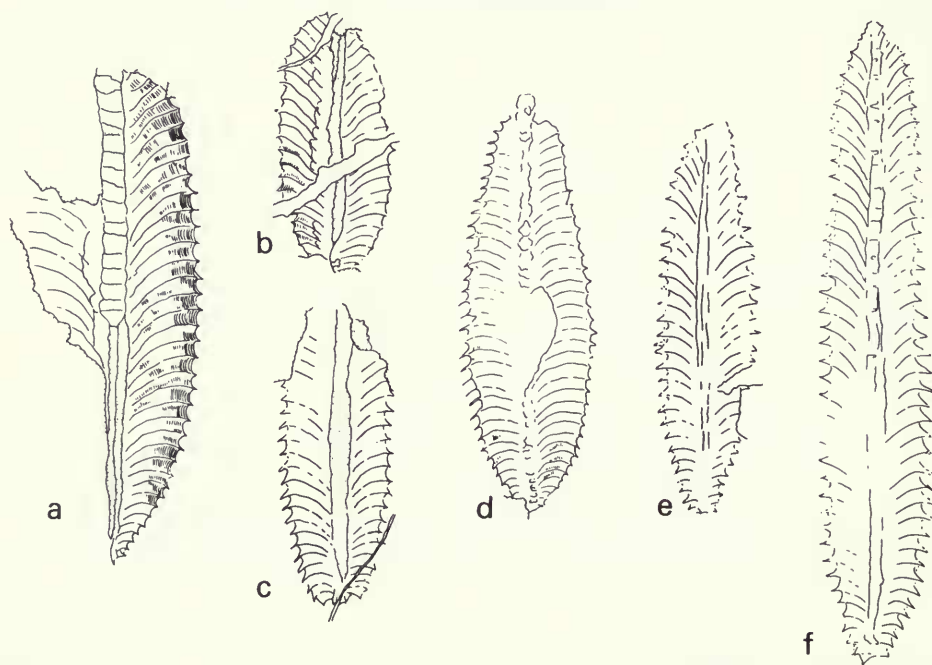


Fig. 48a–c *Pseudophyllograptus angustifolius chors* subsp. nov. a, PMO NF1493, **holotype**, specimen preserved in relief in limestone; upper thecal series broken away exposing, in the lower part of the rhabdosome, the median septa (stippled) which are imperforate, distinguishing the form from *Phyllograptus*, s.s. Growth striations diagrammatic. Olenidsletta Member, 103 m above base. b, NF1548, specimen in full relief in limestone. Olenidsletta Member 100·8 m above base. c, NF1513, showing highly inclined, curved proximal thecae. Olenidsletta Member, 101·9 m above base. All $\times 2$.

Fig. 48d *P. angustifolius* subsp. 1, PMO NF3361, specimen preserved in relief, from 8·5–10 m above base of Olenidsletta Member, i.e. the earliest phyllograptoid in the Spitsbergen sequence; $\times 2$.

Fig. 48e, f *Pseudophyllograptus angustifolius angustifolius* Hall. e, GSC 939a, paratype, flattened, in black shale, figured by Hall (1865: pl. 16, fig. 19). f, GSC 939b, **lectotype**, flattened, in black dolomitic shale, figured by Hall (1865: pl. 16, fig. 21). Both $\times 2$.

- 1895a *Phyllograptus angustifolius* Hall; Holm: 488–489; pl. 14, figs 1–12.
 1902 *Phyllograptus angustifolius* Hall; Elles & Wood: 100–101: pl. 13, figs 7a–f.
 ?1904 *Phyllograptus angustifolius* Hall; Ruedemann: 711–714, text-fig. 37; pl. 15, figs 31–34.
 1936a *Phyllograptus angustifolius* Hall; Bulman: 39–44, text-figs 13–15; pl. 1, fig. 26; pl. 4, figs 7–10.
 ?1947 *Phyllograptus angustifolius* Hall; Ruedemann: 315–316; pl. 53, figs 2–6.
 ?1947 *Phyllograptus angustifolius* var. *magnificus* Ruedemann: 316; pl. 53, fig. 7; pl. 90, fig. 20.

LECTOTYPE. GSC 939b, figured by Hall (1865: pl. 16, fig. 21) and refigured here (Fig. 48f) is here designated **lectotype**. It is held by Geological Survey of Canada, Ottawa.

PARALECTOTYPES. GSC 939, 939a, containing the specimens figured by Hall (1865: pl. 16, figs 17–21), one of which is refigured here (Fig. 48e), together with more than 25 other rhabdosomes. All rhabdosomes are preserved as flattened carbonaceous films; all material held by Geological Survey of Canada, Ottawa.

HORIZON. Several biserial forms are present in slab GSC 939b, including *Pseudoclimacograptus* of *eximius* Ruedemann type, ?*Cryptograptus inutilus* (Hall), together with *Pseudisograptus* (*dumosus* or *nanus*), suggesting Zone D of the Levis succession.

DESCRIPTION OF TYPE MATERIAL. Details of proximal structure and development and of internal rhabdosome structure are unknown. Rhabdosomes are approximately parallel-sided and elongate when mature and are generally tapered to a rounded termination at both proximal and distal ends. The longest rhabdosome, the lectotype, is 42 mm long. Rhabdosomes are generally widest at about 10 to 15 mm from the proximal end and thereafter remain parallel-sided or taper very slightly. Maximum rhabdosome width ranges widely, from 5.5 mm to 8.5 mm; the wider forms tend also to be the longer forms (Fig. 47). Up until the widest point of the rhabdosome, thecae are moderately curved and highly inclined, and they become progressively less inclined, particularly in their initial growth, as the distal rhabdosome margin is approached. Apertural margins are deeply recessed in outline giving a denticulate appearance to the projecting ventral thecal margin. Thecae are spaced $8\frac{1}{2}$ to 12 in 10 mm in the middle third of the rhabdosome, strongly modal at 10–11 (Fig. 49).

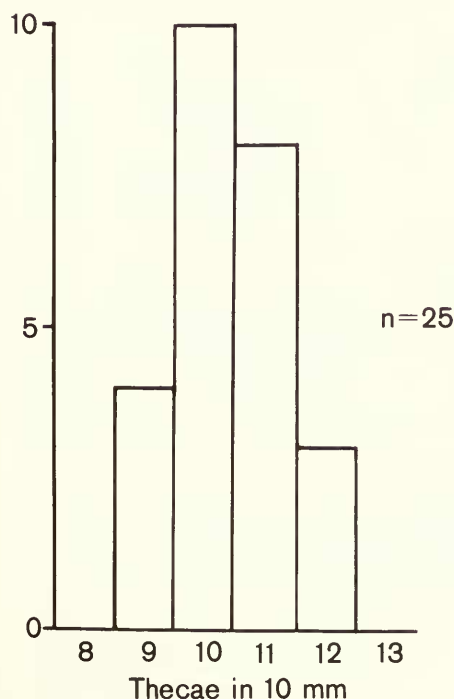


Fig. 49 *Pseudophyllograptus angustifolius angustifolius* Hall, type population; frequency distribution of mature thecal spacing (taken to nearest whole number).

DISCUSSION. The range in thecal spacing is greater than that usually allowed for the species and the mode somewhat lower (e.g. Ruedemann 1947 and Elles & Wood 1902 both give 11–13 thecae in 10 mm). Mature rhabdosomes are readily distinguished by their approximately parallel sides and high inclination of proximal thecae; immature rhabdosomes are distinguished from similar-sized rhabdosomes of *Phyllograptus ilicifolius* by the high initial angle of inclination, and lack of strong curvature, of proximal thecae.

Details of internal rhabdosome structure and proximal development, indeterminable from the type material, can be inferred by reference to the well-known and beautifully preserved material from Sweden, described by Holm (1895), Bulman (1936a) and Skevington (1965). The Swedish material, from Skevington's work, comes from the uppermost *hirundo* Zone of the Orthoceratite Limestone and is accompanied by the earliest diplograptids of the Swedish succession, including *Cryptograptus austrodentatus oelandicus* Bulman, indicating a similar stratigraphic horizon to that of the type material at Levis. Initial thecal budding conforms with the isograptid type of development (Bulman 1936b) and the septa separating the four thecal series in the axial region are complete (Holm 1895) and not perforated as in *Phyllograptus*, s.s. Details of thecal morphology and growth line data are clearly shown by Skevington (1965: figs 14–16).

Although *P. angustifolius* is most widely recorded from strata of latest Arenig or Llanvirn age around the world it is also commonly recorded from the mid or early Arenig (e.g. Texas, Berry 1960; Australia, Thomas 1960; New Zealand, Cooper 1979; England, Jackson 1962; China, Mu *et al.* 1979). The evidence from Spitsbergen, however, suggests that the earlier Arenig forms represent a distinct subspecies and until their detailed morphology is known they should be regarded only as *P. angustifolius*, *sensu lato*.

Because Ruedemann's (1904) figured material is said to come from Beds 2–6 of the Deepkill section it is possible that the earlier subspecies is also embraced by it. Ruedemann's var. *magnificus* from the Blakeley sandstone in Arkansas (of *G. dentatus*, or *P. tentaculatus*, Zone age) appears to differ in no significant way from the nominate subspecies, but the scales given for the two illustrations (1947: pl. 53, fig. 7 and pl. 90, fig. 20) of the cotype are inconsistent and there is thus some doubt about true dimensions and thecal spacing.

Pseudophyllograptus angustifolius chors subsp. nov.

Fig. 48a–c; Pl. 4, fig. 6

STRATIGRAPHIC RANGE. 100·8 to 103·3 m above base of Olenidsletta Member, uppermost V₂ and V_{3a}, Castlemainian.

MATERIAL. **Holotype**, PMO NF1493 (two counterparts, in relief); paratypes PMO NF1446, NF1506–7, NF1513, NF1548, NF1617, NF3295 and several other specimens. Also serially ground specimens PMO NF3174–5.

NAME. 'A walled enclosure,' referring to the enclosure of the sicula within the rhabdosome.

DESCRIPTION. Rhabdosome elongated, oval to elliptical, up to 35 mm long, and 13 mm in maximum width; the width to length ratio is 0·35 to 0·45. In the axial region of the rhabdosome thecae are 1·8 mm in lateral width and moderately transverse in cross section. They are inclined initially at 45° to 55° and curve out to about 90° near their apertures. Their apertural margins are extended into a lip, giving a denticulate appearance in the flattened rhabdosome. Initial thecae are highly inclined. Thecal spacing, measured in 4 specimens only, is 8·5–11 (8·5, 10·5, 11, 11) in 10 mm.

Internally the median septum is unperforated and in cross section is like that described by Holm (1895: pl. 14, figs 11, 12) in the Swedish form; the opposing stipes ²a and ¹b are united over a short lateral distance along their dorsal margins separating the two sides of the cross by a short *b*ar (Fig. 51). The median septum is clearly exposed in the lower half of the holotype, PMO NF1493 (Fig. 48a).

DESCRIPTION OF SECTION SERIES. The proximal end of specimen NF3175 was serially ground at intervals ranging from 0·02 to 0·05 mm, and the ground surfaces were drawn under camera

lucida and photographed. An excellent series of sections resulted revealing the proximal structure and development of the rhabdosome. A selection of these is shown in Fig. 50.

Overall sicula length is a little greater than that represented in the ground section series, i.e. about 1.8 mm; dorsoventral width of the sicula is 0.2 mm; lateral width 0.15 mm near the

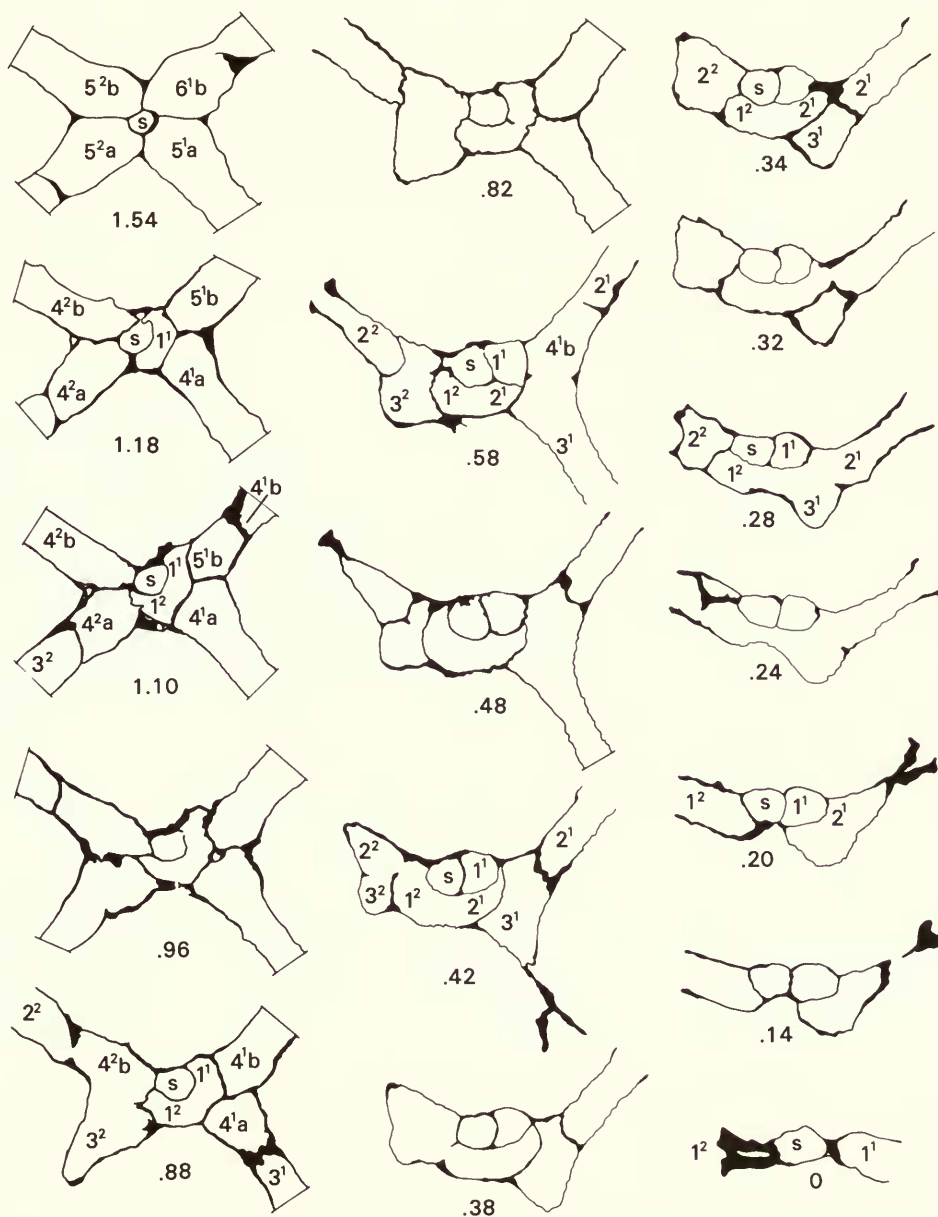


Fig. 50 *Pseudophyllograptus angustifolius chors* subsp. nov. Selected serially ground sections through the proximal region of specimen PMO NF3175, from 100.8 m above base of Olenidsletta Member, type section; $\times 17$. Section level indicated by number (in millimetres) above basal section. The highest section, at 1.54 mm above base, shows the sicula entirely enclosed by thecae 5²a, 5²b, 6¹b and 5¹a (hence *chors*, enclosure). The foramen between th1² and th2¹ extends from about section 1.18 to section 0.58, that is for 0.4 mm. Note that the distal portions of thecae 1¹ and 1² lie medially between the sagittal planes of the four thecal series (stipes) as seen in higher sections (e.g. section 1.54).

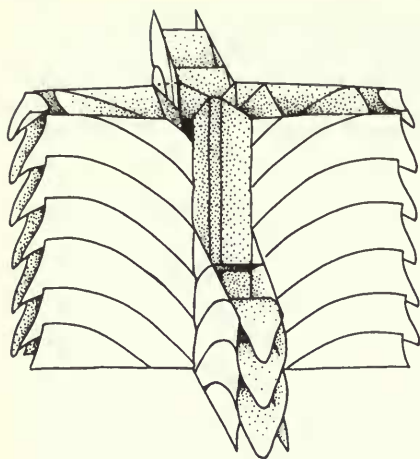


Fig. 51 *Pseudophyllograptus angustifolius chors* subsp. nov. Cut-away diagram showing internal rhabdosome structure.

aperture. The ventral side of the sicula was not determined and it is not known on which side of the sicula the first theca develops. Theca 1¹ arises 0.36 mm below the apex of the sicula and, at 0.56 mm from the apex, expands to envelop about half of the sicula (in transverse section; Fig. 50, section 1.18). Theca 1² arises high on th1¹ and the 1¹/1² interthecal wall appears at about 1.0 mm from the apex of the sicula. Thecae 1¹ and 1² then grow in contact with the sicula to the level of the sicular aperture, where they turn abruptly outwards to become horizontal. The insertion of subsequent thecae, as inferred from the section series, is shown in the thecal diagram (Fig. 52). Initial development is dextral and isograptid, with th1² dicalycal. On the stipe¹ side the dicalycal theca, th3¹, is right-handed and dichotomy is isograptid. On the stipe² side, the dicalycal theca 3² is left-handed and dichotomy is also isograptid. Development of the rhabdosome thus follows the same plan as that of *Tetragraptus bigsbyi* (Bulman 1970).

Thecal budding sequence differs from that described by Bulman (1936a) in *P. angustifolius angustifolius* from the Orthoceras Limestone of Sweden, where the two second-order dichotomies were thought to conform with what is here termed the *artus* type of division rather than isograptid as described here. However, Bulman's interpretation was based on a comparison with *T. bigsbyi* which has since (Bulman 1955, 1970) been reinterpreted. If *Phyllograptus angustifolius* is similarly reinterpreted then its thecal budding sequence conforms with that described here.

In the initial downward growth of thecae 1², 2¹ and 2², the Spitsbergen form differs from that of Sweden (Bulman 1936a: text-fig. 15), where these thecae are shown as having no initial downward component of growth. A further difference lies in the way the sicula becomes entirely enclosed within the rhabdosome during its scandent development (hence *chors*, enclosure) rather than remaining, as a protruding structure, along the lateral wall at the junction of stipes 1^b and 2^b (compare Bulman's sections in his text-fig. 13B with those given here in Fig. 50).

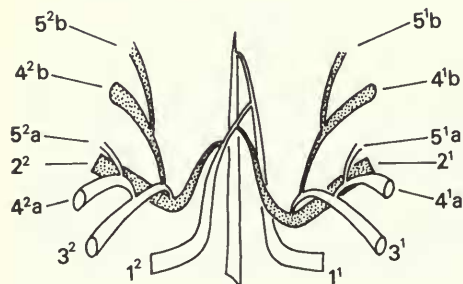


Fig. 52 *Pseudophyllograptus angustifolius chors* subsp. nov. Thecal diagram; stipes 1^b and 2^b stippled.

DISCUSSION. There appears to be a much more limited range of variability of rhabdosome shape and proportions than in *Phyllograptus typus*. The new subspecies is based on differences in proximal structure compared with the Swedish *P. angustifolius angustifolius* as described above. In his discussion of the Swedish subspecies Bulman (1936a) found several points of difference in proximal development and structure from *Tetragraptus bigsbyi* and concluded that the latter was unlikely to be the ancestor of the former. The Spitsbergen form conforms much more closely to *T. bigsbyi*, as interpreted by Bulman (1970), and a reclined tetragraptid of *bigsbyi* type is a feasible ancestor for it.

The Swedish and Spitsbergen forms, along with the form described here as subsp. 1, are all referred to Hall's species *angustifolius*, implying that the total range of the species *s.l.* is from lower Arenig to topmost Arenig or basal Llanvirn. However, it is quite possible that, as the pseudophyllograptid rhabdosome represents merely a reclined tetragraptid with its stipes united along their dorsal margins, it has been repeatedly derived from tetragraptid ancestors at different times. Such a derivation would, if it could be proved, carry important implications for taxonomy and nomenclature of the group.

Pseudophyllograptus angustifolius subsp. 1, nov.

Fig. 48d; Pl. 4, fig. 8

STRATIGRAPHIC RANGE. The only specimen comes from the 8.5–10 m interval in type section, Olenidsletta Member V₁b.

MATERIAL. PMO NF3361a and b (counterparts), well preserved in semirelief.

DISCUSSION. The form differs from *Pseudophyllograptus angustifolius chors* subsp. nov. only in the less curved and more highly inclined thecae, particularly noticeable in the distal part of the rhabdosome. However, because the specimen comes from an earlier horizon than is generally recorded for *P. angustifolius*, *s.l.*, and the Spitsbergen section is separated from other pseudophyllograptids by a considerable gap (Fig. 1, p. 161), it seems unwise to include them in *P. angustifolius chors* and so greatly extend the range of that subspecies. It is probably a distinct subspecies but is best left in open nomenclature because little is known of its proximal structure.

Genus *PSEUDOTRIGONOGRAPTUS* Mu & Lee, 1958

TYPE SPECIES. *Graptolithus ensiformis* Hall 1865.

DISCUSSION. The taxonomic history of the graptolites that were formerly included in *Trigonograptus ensiformis* (Hall) is complicated. Jackson & Bulman (1970) showed that the holotype of the type species of *Trigonograptus*, *T. lanceolatus* Nicholson, was a specimen of *Didymograptus* preserved in an unusual way. *Tristichograptus* was proposed as a new name, with the well-known species *T. ensiformis* (Hall) as type species. Fortey (1971) described some beautifully preserved isolated material attributed to *T. ensiformis* from the Valhallfonna Formation, which had a unique triserial scandent arrangement of the stipes. He indicated that the genus *Pseudotrigonograptus* Mu & Lee 1958 (type species, *M. uniformis* Mu & Lee 1958) might prove to be a senior synonym of *Tristichograptus*. Rickards (1973) accepted this, and essentially synonymized most of the described species of *Trigonograptus* with *T. ensiformis* (Hall), including the designated type species of *Pseudotrigonograptus*. So in Rickards' opinion the type species of *Pseudotrigonograptus* is *P. ensiformis* (Hall). Our additional material from Spitsbergen represents triserial and quadriserial forms of 'ensiformis' type, both of which have previously been reported from China (Mu & Zhan 1966). The quadriserial form makes its first appearance, as one might expect, just below the earliest triserial form. We believe that the quadriserial 'ensiformis' deserves specific distinction from the triserial one. The problem is that the usual mode of preservation of the flattened material, which is essentially along the septum between thecae, showing no apertures (Fortey 1971: fig. 2), does not reveal direct evidence of the whole form of the rhabdosome. In our opinion the unifying character of these graptolites is the side-by-side arrangement of the scandent stipes, which is unlike the cruciform

disposition of *Phyllograptus* and *Pseudophyllograptus*, and indicates a monophyletic origin of both three- and four-stiped scandent forms. Regardless of the number of species the valid generic name is *Pseudotriconograptus*. The four-stiped form is both wider (across two rows of thecae) and longer than the three-stiped form; the type material of *T. ensiformis* (Hall) is of this kind, and probably had four series of thecae (Rickards 1973). The nearest flattened dimensions to those of the triserial form are those of *T. ensiformis minor* (Mu & Lee 1958), as Fortey (1971) noted, and *P. minor* is used as a specific name here. The obvious disadvantage in using specific nomenclature based on flattened specimens is that no apertural characters are known in such forms. We prefer, nonetheless, to use established names rather than propose a 'parallel' nomenclature for species known from relief or isolated material. We consider that Rickards' wide view of *P. ensiformis* was incorrect and that there are at least two, and possibly more, species in *Pseudotriconograptus*. Flattened or unflattened this curious and aberrant graptolite is of considerable stratigraphical use.

Pseudotriconograptus ensiformis (Hall 1865)

Fig. 53a–d

Synonymy in Rickards (1973), excluding the triserial forms included in *P. minor* below.

STRATIGRAPHIC RANGE. Upper part of Olenidsletta Member, V₂b, 102–103 m from base of Member, just below earliest *Isograptus victoriae victoriae* assemblages, and probably base of Castlemainian Ca₂ (= base of *D. hirundo* Zone).

MATERIAL. PMO NF74, NF1493a, NF3389.

DISCUSSION. Two specimens in relief clearly show the quadriserial, scandent nature of this species. The same habit was deduced from topotype specimens of *P. ensiformis* from Quebec described by Rickards (1973), and because our material agrees in other characters the Spitsbergen form is placed in the same species. The broader of our two relief specimens measures 3 mm across the trace of the median septum indicating that this species can be stouter than *P. minor*. The other specimen is 2.3 mm across, which is within the range of variation of the triserial form. Rickards noted that the cross section of this species was an ellipse, rather than circular, and that the shorter diameter of the median septum therefore probably belongs to the shorter axis of cross section. Unlike the topotype specimens ours show some well-preserved thecal apertures (Fig. 53a) which like the triserial species are quite deeply excavated with broad, spoon-like lips. Thecae protrude only about 1.1 mm from the area of common contact with the adjacent thecal series, so that the whole rhabdosome is very compact, and quite unlike *Pseudophyllograptus* in its organization. This leads us to the reconstruction of the cross section of *P. ensiformis* shown in Fig. 53d. Thecal spacing is 10–11 in 10 mm distally. Neither of our specimens is complete: the larger of the two is almost 2 cm long, and was certainly longer when complete, supporting the observation that *P. ensiformis* grew to a larger overall size than *P. minor*.

Mu & Lee (1958) placed *Pseudotriconograptus* in the family Phyllograptidae. *Pseudotriconograptus* exhibits none of the proximal end characters typical of the Phyllograptidae, as revised in this work (p. 273; *Phyllograptus*, *Xiphograptus* gen. nov.). Fortey (1971) showed that the triserial form has an initial development of normal isograptid type. Its affinities more probably lie with *Isograptus* and the Dichograptidae, rather than with *Phyllograptus*. Despite the similarity in habit there is nothing to suggest that *Pseudophyllograptus* is particularly close to *Pseudotriconograptus*, although both are typically dichograptid in development, and we consider it possible that these genera had independent origins from tetragraptid ancestors. There is no stratigraphical evidence relevant to the origins of *Pseudotriconograptus*: it appears suddenly and cryptogenetically late in the Arenig, and extends through the Llanvirn. This is a long range, and it would be surprising if the single species *P. ensiformis* were the only one through this time interval. However, the difficulties of recognizing true specific characters from the trace of the median septum alone leads us, like Rickards (1973), to take a very wide view of the species with quadriserial, scandent habit.

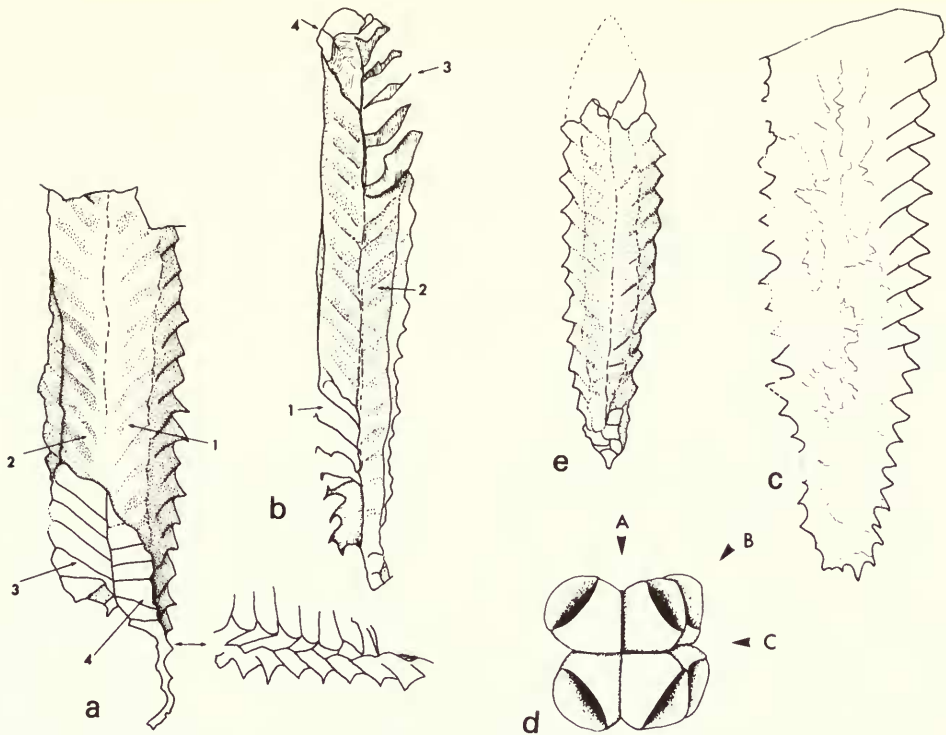


Fig. 53a-c *Pseudotrigonograptus ensiformis* (Hall). a, PMO NF1493a, specimen preserved in full relief, showing the four series of thecae (1-4) and thecal apertures. This is the wide '*Trigonograptus*' mode of preservation shown in Fig. 53d(C). Detail on right shows the lateral view of thecal series 1 and 4 at lower end of stipe. 103 m from base of Olenidsletta Member. b, NF74, showing narrow '*Trigonograptus*' mode of preservation, as in Fig. 53d(A); thecal series 1-4 indicated. 102 m above base of Olenidsletta Member on Profilstranda. c, NF3389, flattened in shale, preserved in 'apertural' aspect as in Fig. 53d(B). Note short interthecal septa unlike *Pseudophyllograptus*; broad belt of periderm in centre may represent crushed, upper, thecal series. Same horizon as b. All $\times 4$.

Fig. 53d Reconstructed cross section of four-stiped *Pseudotrigonograptus*. Flattening, or splitting, in the three directions indicated account for the three preservation modes shown in the series, Fig. 53a-c above; A and C result in splitting along the median 'septum' (short and long respectively) and B results in the apparently biserial mode, with maximum width and full thecal profiles.

Fig. 53e *Pseudotrigonograptus minor* (Mu & Lee). PMO NF3388, typical specimen preserved in relief, with third thecal series removed to show median 'septum' (120° angle between two remaining series). 107 m above base of Olenidsletta Member; $\times 4$.

Flattened specimens found in a shaly bedding plane at the same horizon as relief *P. ensiformis* are certainly referable to this species. It might be possible to mistake them for *Phyllograptus* or *Pseudophyllograptus*, but their identity is betrayed by the very short length of the interthecal septa, with a broad, undifferentiated 'axis', and the low inclination of the thecae (distal inclination of phyllograptoids is always at right angles to the axis of the stipe). If our view of the cross section is correct this flattened material showing the apertures in equal profile should result from flattening in the 'phyllograptoid' mode, with one pair of thecal series normal to the bedding plane, so that the rhabdosome does not get the chance to split along the median septum, as in the usual preservation (Fig. 53d - 'B'). These specimens are 5 mm broad: forms with similar dimensions were described by Cooper (1979: 93) as 'graptoloid genus 1 sp. 3'.

Pseudotrigonograptus minor (Mu & Lee 1958)

Fig. 53e; Pl. 5, fig. 13

- 1953 *Glyptograptus* aff. *dentatus* (Brogniart); Spjeldnaes: 180; pl. 1, figs 12, 13.
 1953 *Glossograptus* aff. *acanthus* Elles & Wood; Spjeldnaes: 181; pl. 1, fig. 7.
 1958 *Trigonograptus ensiformis* var. *minor* Mu & Lee: 396, text-fig. 3.
 1971 *Tristichograptus ensiformis* (Hall); Fortey: 188–199; pls 26–29; text-figs 1–5.
 1979 Graptoloid gen. 1 sp. 1; sp. 2; Cooper: 93; pl. 19d, f; text-fig. 84a.

STRATIGRAPHIC RANGE. Upper part of Olenidsletta Member, V₂b–V₃, 102 m to top, and in basal bed of Profilbekken Member. Late Arenig, Castlemainian (Ca₂ to Ca₃), and probably *D. hirundo* Zone equivalent.

MATERIAL. Full range of the material is given in Fortey (1971). PMO NF3385, NF3388 are additionally figured here.

DISCUSSION. This species was described at length by Fortey (1971) from superb isolated material, and repetition is unnecessary here. Cooper (1979) found flattened specimens which show that thecal apertures can be displayed if the graptolite is compressed *in toto*. The more usual mode of preservation is that illustrated in Fortey (1971: text-figs 1c, 2) where the rhabdosome splits along the median septum to present that aspect which lacks apertures. Because the cross section of *P. minor* is nearly circular there is no strongly preferred orientation in flattened material. Two series of apertures are usually visible, but if the boundary wall between the thecae is presented on one side, then the effect is to produce a puzzling-looking graptoloid with only one series of thecal apertures visible (e.g. Cooper 1979: pl. 19d, specimen on right). These flattening properties are explained by the triserial nature of the rhabdosome. Similar properties are shown by the specimens figured by Spjeldnaes (1953) from the *D. hirundo* Zone of Norway, which were wrongly interpreted by him as biserial, scandent forms.

Triserial rhabdosome habit characterizes whole populations; it seems to be a reliable specific characteristic for this reason. Which of a number of specific names proposed by Mu & Lee (1958) to apply to it is more difficult. The width across the median septum presented in the usual mode of preservation is variable, but most specimens are close to 2 mm across any two series of thecae, and the mean value for our population is 2.3 mm. Although the largest specimens are about 2 cm long (e.g. Fortey 1971: pl. 29, fig. 3a) the mean value is 1.5 cm. These proportions are within the range of *Trigonograptus ensiformis* var. *minor* Mu & Lee (1958), and this name seems to be the best available to describe the triserial *Pseudotrigonograptus*, although nothing like the same thecal detail is known from the Chinese material, which is from the *Didymograptus hirundo* Zone of the Ningkuo Shale. Relief material is readily distinguished from the quadriserial species because the angle between adjacent thecal series is 120°, whereas the median septa on the latter intersect at 180°.

Subfamily ISOGRAPTINAE Harris, 1933

DIAGNOSIS. Sricula and proximal thecae relatively long; development of isograptid type, dextral or rarely sinistral, sricula and th1' symmetrically developed (isograptid symmetry); single dichotomy produces two reclined to scandent stipes, united (biserial) in some scandent forms; thecal inclination initially low or high, distally generally high.

DISCUSSION. Harris's (1933) concept of the Family Isograptidae incorporates the genera *Isograptus* Moberg 1892, *Pseudisograptus* Beavis 1972, *Oncograptus* T. S. Hall 1914, *Cardiograptus* Harris & Keble, in Harris 1916, *Skiagraptus* Harris 1933 and *Maeandrograptus* Moberg 1892. His phyletic scheme linking these genera has been revised by Cooper (1973) on the basis of a population study of the group. The *I. victoriae* lineage is regarded as ancestral to both the group with *I. caduceus* and related forms including *Skiagraptus* (*sensu* Harris 1933, *non* Whittington & Rickards 1969), and the *Pseudisograptus* group. There is thus a good phylogenetic basis for distinguishing the group at subfamily level. All members of the plexus possess isograptid symmetry.

The phyletic position of *Oncograptus* and *Cardiograptus* is less certain; they both possess isograptid symmetry and, as Harris pointed out, many other isograptid features but intermediate forms are lacking. In particular the inclusion of *Oncograptus* must remain provisional in view of its apparently anomalous development (Bulman 1936b). *Maeandrograptus* (*sensu* Cooper 1973: 57) is excluded from the group and from the subfamily on the grounds that it lacks isograptid proximal symmetry.

The earliest Australasian isograptid, *Isograptus primulus* Harris, appears in the Chewtonian, immediately before the 'burst' of isograptids of the *I. victoriae* lineage in the Castlemainian. Harris regarded *I. primulus* as ancestral to *I. victoriae lunatus* and hence as the progenitor of all later Australasian isograptids. However, there are no transitional populations linking *primulus* and *lunatus* and Cooper (1973) has shown that the changes in passing from *primulus* to *lunatus* (the earliest member of the *victoriae* lineage) have no continuity with the changes involved in the transition from *lunatus* to *victoriae* and later forms. *I. victoriae lunatus* was suggested to have been derived from a reclined didymograptid ancestor by the acquisition of isograptid symmetry, whereas the earlier *I. primulus* was not thought to be closely related to the *victoriae* group and its descendents. Its closest ally was suggested to be the Swedish *I. gibberulus* of Bulman (1932), to which should now be added *I. scandens* sp. nov. from Spitsbergen. *I. victoriae lunatus* and the *I. primulus* group thus do not share an immediate common ancestor and belong to distinctly different lineages. Evolution of the isograptid rhabdosome probably occurred twice.

A phyletically-based classification would thus require two separate major groups. The first would include *I. primulus*, *I. scandens* and the Swedish *I. gibberulus*, and the second would comprise *I. victoriae* and its descendents including *Pseudisograptus*, *Skiagraptus* and, provisionally, *Apiograptus* Cooper & McLaurin 1974, *Kalpinograptus* Qiao 1977, *Apoglossograptus* Finney 1978 (*nom. nud.*; probably = *Kalpinograptus*) and *Exigraptus* Mu, in Mu *et al.* 1979 (with secondary loss of isograptid symmetry?). Furthermore the two groups could not be embraced by the one subfamily since they are inferred to have been independently derived from dichograptoid ancestors. This means that if a family-group name is maintained for the *I. victoriae-caduceus-Pseudisograptus* plexus then a new genus and subfamily name is needed for the '*I. primulus* group'.

The concept of isograptid development was based on the Swedish *I. gibberulus* (*sensu* Bulman 1932), i.e. on the *primulus* group. However, it is now clear that *both* groups possess isograptid development and symmetry and it is immaterial, for the appropriateness of the term isograptid development, to which group the name *Isograptus* (and Isograptinae) should eventually apply. The two groups represent an example of parallel evolution, a phenomenon that we suspect is commonplace among dichograptoids. The one character that serves to distinguish between the two is thecal inclination; in the *primulus* group thecae throughout the rhabdosome are inclined at a high angle to the dorsal stipe margin from their origins to their apertures whereas in the *victoriae* group all thecae beyond those of the proximal region commence their growth at a low angle to the dorsal stipe margin but curve around to achieve high inclination only in the apertural region.

The next question that arises is, to which of the two groups does Nicholson's (1875) *Didymograptus gibberulus*, the type species of the genus *Isograptus*, belong? Little can be determined from Nicholson's (1875: pl. 7, figs 3, 3a-b) and Elles & Wood's (1902: text-fig. 33a-b; pl. 2, figs 9b, d) figures of the type specimens except that they are unlikely to represent the same species as Holm's material figured by Bulman (1932: pl. 8, figs 1-5). Their relationship to the two groups cannot be determined until the type specimens have been redescribed and a lectotype designated. From his re-examination of the type specimens C. J. Jenkins (personal communication) has concluded that at least two species are represented. It is clearly unwise to formalize the two groups at this stage.

The Subfamily Isograptinae Harris is therefore provisionally retained here for the diphyletic grouping of all the 'isograptid' genera listed above. Isograptid proximal symmetry is a character of the group but is *not* a synapomorphy for the group. It has been acquired independently at least twice.

Genus *ISOGRAPTUS* Moberg, 1892

DIAGNOSIS. Reclined to scandent biramous graptoloids with isograptid development and symmetry.

TYPE SPECIES. *Didymograptus gibberulus* Nicholson 1875.

DISCUSSION. From the foregoing discussion of the Subfamily Isograptinae it is clear that the genus *Isograptus* needs redefinition. It is used here in its diphyletic sense to include reclined biramous dichograptoids with isograptid symmetry.

Representatives of each of the two groups are present in the Spitsbergen succession. The *primulus* group is represented by *I. scandens* sp. nov. which is found in the *D. protobifidus* Zone (Chewtonian), and the *victoriae-caduceus* plexus is represented by *I. victoriae victoriae*, *I. v. maximus*, and *I. caduceus imitatus*, in Castlemainian beds.

Only one horizon – the 110 m level with *I. v. victoriae* – has a reasonably large sample population and it is not possible to analyse the Spitsbergen isograptids from the point of view of population systematics for comparison with the Australasian populations (Cooper 1973). In terms of the populations approach, the various subspecies are regarded as successive populations with wide, overlapping, ranges of variability. This means that one often cannot assign a solitary specimen to a particular subspecies because it lies in the overlap zone of two successive subspecies. However, if several specimens from a single locality are available, a much greater degree of precision in identification is available. The morphotype approach (Harris 1933; Beavis & Beavis 1974), on the other hand envisages the subspecies as having a non-overlapping range of morphological variation, but overlapping stratigraphical ranges. We prefer the populations approach because it is consistent with the biological concept of species.

Isograptus caduceus imitatus Harris 1933

Fig. 54a–d

1933 *Isograptus caduceus* var. *imitata* Harris: 92, figs 55–59.

1973 *Isograptus caduceus imitatus* Harris; Cooper: 71–74, text-figs 14a–i.

1976 *Isograptus* aff. *caduceus imitatus* Harris; Fortey: 278, text-fig. 7.

STRATIGRAPHIC RANGE. Upper Olenidsletta Member V₃, and basal beds of Profilbekken Member, 125–145 m above base of Olenidsletta Member, upper Castlemainian.

MATERIAL. PMO NF1739 (flattened); NF3332–3, SMA 109734–5 and several other specimens (in full relief).

DESCRIPTION. Rhabdosome is V-shaped rather than U-shaped, the dorsal stipe margins flexing sharply upwards rather than smoothly as in *I. victoriae victoriae*. The sicula ranges from 3.4 to 4.2 mm in length and is about 0.7 mm wide at the aperture. The ventral notch between the free ventral walls of the sicula and theca 1¹ is, in most specimens, narrower and deeper than in *I. victoriae victoriae*. The outline of the ventral margin is deeper in the proximal region than it is in *I. victoriae victoriae*, resulting from the ventrally extended sicula and proximal thecae. This feature is most marked in the specimen from the 125 m level (Fig. 54a) in which the ventral margins of the sicula and first theca project outwards in prominent ventral processes. The specimen is preserved as a flattened rhabdosome in black calcareous shale, in contrast to specimens from the 128–129 m level which are preserved in full relief in limestone. In the absence of an adequate population from the 125 m level it is not possible to assess the significance of this difference except to point out that the feature is one that is unlikely to be greatly enhanced by the flattening process.

The stipes are widest at their origin and gradually taper throughout their length. Proximal stipe width ranges from 2.1–2.3 mm, and maximum stipe length observed is 8 mm. Pendent thecae number 6–8. Thecae midway along the length of the stipe are inclined initially at about 30°; they curve strongly so that their free ventral walls are inclined at about 110°.

DEVELOPMENT. Details of the proximal region can be clearly seen in a few specimens from the 128–129 m level. In most specimens (Fig. 54b) proximal development follows closely that

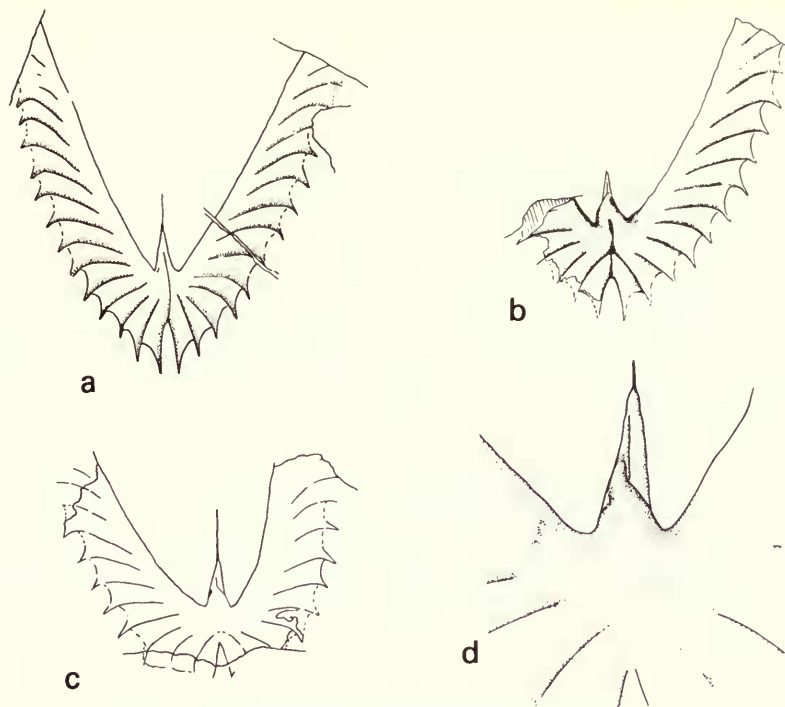


Fig. 54 *Isograptus caduceus imitatus* Harris. a, PMO NF1739, specimen with pronounced V-shape, flattened, resembling lectotype, from 125 m level, Olenidsletta Member, southern section; $\times 5$. b, NF3333, specimen in relief in limestone clearly showing dextral development mode (isograptid type) and an apparent median furrow between $th1^2$ and $th2^1$. 128–9 m level, Olenidsletta Member, type section; $\times 5$. c, d, NF3332, specimen in relief ($\times 5$) and enlarged ($\times 15$) proximal region, clearly showing sinistral development mode. Same horizon as b.

described in *I. victoriae victoriae* with $th1^2$ and $th2^1$ growing downwards and expanding to form a manubrium-like structure before flexing sharply to commence upward growth. Theca 1^1 originates near the apex of the sicula and $th1^2$ at about 0.7 mm below the sicula apex. In the specimen shown in Fig. 54b a median furrow separating $th1^2$ from $th2^1$ extends upwards from the isograptid arch; it possibly indicates the presence of an internal septum between the two thecae, in which case the crossing canal is restricted to a small opening near the dorsal margins of the two thecae.

Development type and mode were determined in two specimens. In the first it is of dextral mode and isograptid type (Fig. 54b). In the second (Fig. 54c), however, development mode is clearly seen to be sinistral; in all other respects it resembles the normal dextral development. The relative frequency of sinistral development is unknown. Both specimens are from the 128–129 m level.

DISCUSSION. The specimen (Fig. 54a) from the 125 m level matches the lectotype (Cooper 1973: text-fig. 14i) reasonably well, whereas those from the 128–129 m level, with more rounded ventral outlines in the proximal region, best match New Zealand specimens from the upper Castlemainian. The Spitsbergen material from the two horizons, together with the incomplete specimen (Fortey 1976: text-fig. 7) from the basal Profilbekken Member, are all here referred to *I. caduceus imitatus*. Those specimens of the preceding *I. victoriae victoriae* in the Spitsbergen sequence with somewhat V-shaped outlines and projecting sicula and $th1^1$ (Fig. 55b) closely resemble members of *I. caduceus imitatus*, such as that figured in Fig. 54b, with relatively rounded ventral margins consistent with the inferred derivation of the *caduceus*

group from the *victoriae* lineage (Cooper 1973). What is surprising in the Spitsbergen succession is that the one specimen from the 125 m level (Fig. 54a) is more like the later (upper Ca₃ and Ya₁) Australasian *imitatus* than are specimens from the overlying 128–129 m level (Figs 54b–d).

The discovery of a specimen with sinistral development is intriguing. Alternative sinistral and dextral development has been reported in *Tetragraptus serra* by Bulman (1936a) and in the dendroids *Dictyonema flabelliforme*, *Clonograptus tenellus* and *Adelograptus hunnebergensis* by Stubblefield (1929); in all of these species dextral development predominates over sinistral (see Hutt's (1974) comments on *C. tenellus* and *A. hunnebergensis*). Specimens with sinistral development appear to be identical with their dextral counterparts in the same bedding planes in all other respects and there seems no reason to suspect that they were not part of the same population. This would imply that they are polymorphic variants and that the astogenetic rhabdosome development programme of an individual colony can be switched from dextral to sinistral without seriously affecting other aspects of development, at least for those species listed above.

The discovery of sinistral development in an isograptid also goes some way towards resolving the problem of deriving the *Oncograptus* rhabdosome from an isograptid ancestor as suggested by Harris (1933). Bulman's (1936b) study of *Oncograptus* showed it to be distinguished from isograptids (and from most dichograptids) in three ways: sinistral development mode, *artus* development type, and possession of an 'extra' theca (th2'b). Sinistral development would not necessarily now imply preclusion of an isograptid ancestor but the two other objections remain.

Isograptus victoriae victoriae Harris 1933

Fig. 55a, b; Pl. 5, fig. 10

1933 *Isograptus caduceus* var. *victoriae* Harris: 90, figs 7–10.

1973 *Isograptus victoriae victoriae* Harris; Cooper: 62–63, text-figs. 9a–f.

1976 *Isograptus victoriae victoriae* Harris; Fortey: 276–277; text-figs 5a–c.

STRATIGRAPHIC RANGE. Upper Olenidsletta Member, V₃, 107–110 m above base, Castlemainian.

MATERIAL. NF1634, NF1647, NF3047 and more than 20 other specimens. All are preserved in full relief in limestone but, unfortunately, disintegrate when isolated by acid solution.

DESCRIPTION. The rhabdosome is U-shaped, the dorsal stipe margins of most specimens curving smoothly away and upwards from the sicular 'wedge'. The stipes reach about 10 mm in

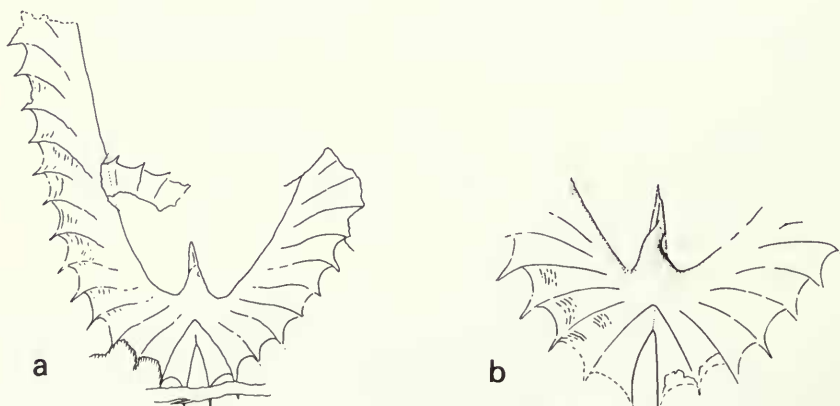


Fig. 55 *Isograptus victoriae victoriae* Harris, rhabdosomes preserved in relief in limestone. a, PMO NF1647, incomplete mature rhabdosome in which proximal thecae have slightly sigmoidal curvature; $\times 5$. b, NF3331, proximal portion showing isograptid, dextral, development; $\times 6.5$. Both from 110 m above base of Olenidsletta Member, type section.

length. The sicula ranges from 3.3 to 4.1 mm (mean value 3.6 mm) in length, and is about 0.7 mm wide at the aperture. The ventral 'notch' between the free ventral margins of the sicula and first theca is relatively narrow and deep and, in a few specimens, is partially filled in by a film of periderm (Fortey 1976: 277). There are 5–7 pendent thecae (*sensu* Cooper 1973).

The sicula and first theca protrude ventrally slightly more than in their Australasian counterparts which have a more rounded ventral rhabdosome margin in the proximal region. Otherwise general rhabdosome shape matches well with the Australasian material.

Stipes are parallel-sided or taper very slightly. Stipe width in the proximal region ranges from 1.9–2.5 mm (mean 2.17 mm). Thecal curvature agrees well with that in Australasian forms except for slight recurvature (particularly in the proximal region) resulting from the initial direction of thecal growth being lateral rather than strictly towards the ventral rhabdosome margin (Fortey 1976: 277). Frequency distributions of sicula length, number of pendent thecae and proximal stipe width are shown in Fig. 56.

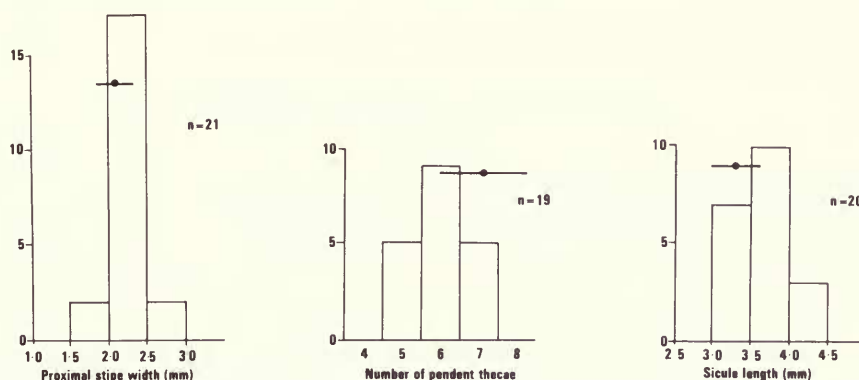


Fig. 56 *Isograptus victoriae victoriae* Harris. Frequency distribution of proximal stipe width and sicula length (taken to nearest whole number) and number of pendent thecae in the population of *I. victoriae victoriae* from the 110 m level in the Olenidsletta Member. The mean value and one standard deviation from the mean for equivalent Australasian samples (from Cooper 1973: 62) is shown for each character.

DEVELOPMENT. Development type and mode can be clearly seen in eight specimens from the external morphology of the proximal region (Fig. 55a). The point of origin of $th1^1$ lies very high on the ventral side of the sicula. Theca 1^2 originates from $th1^1$ about 0.75 mm below the apex of the sicula, that is about 0.85 mm above the level at which the dorsal stipe margins diverge from the sicular 'wedge'. It rapidly swells into a conspicuous bulge and expands laterally to mask the sicula and $th1^1$ completely, as observed from the reverse side of the rhabdosome. Theca 2^1 arises from $th1^2$ via an apparently broad 'crossing canal'. Development in all eight specimens is thus of isograptid type and of dextral mode, as in the Swedish *I. gibberulus* (Bulman 1932: 23–25).

The origin of the stipes (i.e. origins of $th1^2$ and $th2^1$) is rather higher on $th1^1$ than was previously inferred (Cooper 1973: text-fig. 4) in the flattened Australasian material, giving the stipes a greater initial downward component of growth. It is also clear from the Spitsbergen specimens that the base of the supradorsal sicular 'wedge' is broadened by the proximal portions of thecae 1^2 and 2^1 , a feature that becomes greatly exaggerated in the manubriate species (*Pseudisograptus*), thought to have been derived from the *victoriae* lineage at about the *maximus* level.

DISCUSSION. The frequency distributions of sicula length, number of pendent thecae and proximal stipe width match well with the mean value and one standard deviation from the mean of the Australasian populations (Fig. 56).

The well-preserved Spitsbergen material shows several details of morphology and development not seen in the Australasian material, all of which is flattened. The subspecies is the first of the *I. victoriae* lineage to appear in the Spitsbergen section, and is found in great abundance at the 110 m level. The slightly deepened ventral rhabdosome margin in the proximal region (rather than a smoothly rounded margin as in Australasian *victoriae*) is a feature which becomes prominent in the *Isograptus caduceus* lineage, suggesting that the Spitsbergen population may be displaced towards the *caduceus* end of the *victoriae* spectrum. Although separation of the *caduceus* lineage does not appear to become complete until the Castlemainian (about *maximodivergens* level, judged from the Australasian sequence) Australasian populations of the earlier forms, *lunatus*, *victoriae* and *maximus*, contain end members with 'V-shaped' rhabdosomes which were taken as evidence supporting the *victoriae* origin of the *caduceus* lineage (Cooper 1973: 104). The Spitsbergen populations from both the 110 m level (*victoriae*) and 125–129 m level (*imitatus*) provide further supporting evidence and suggest that some degree of geographic isolation may have been involved in the splitting (cladogenesis) event. Relationship of *victoriae* and *imitatus* in the Spitsbergen sequence is discussed under *imitatus*.

Isograptus victoriae maximus Harris 1933

Fig. 57

1933 *Isograptus caduceus* var. *maxima* Harris: 91, fig. 13.

1973 *Isograptus victoriae maximus* Harris; Cooper: 63–65, text-figs 10a–e.

1976 *Isograptus victoriae maximus* Harris; Fortey: 277, text-fig. 6a–b.

STRATIGRAPHIC RANGE. Upper beds of the Olenidsletta Member, from 130 m above base to top, and basal bed of the Profilbekken Member.

MATERIAL. PMO NF1809, and several incomplete specimens.

DISCUSSION. The figured specimen was noted by Fortey (1976: 277) to match the Australasian modal forms well. Sicular length is 4.5 mm, proximal stipe width is 2.8 mm, distal stipe width is 3.5 mm, and there are about 10–12 pendent thecae. Secondary periderm has been deposited in the apex of the ventral indentation between the sicular and first theca and in the axial region on either side of the sicular 'wedge'. Development details cannot be seen as the specimen is preserved in obverse view, but proximal structure is consistent with an isograptid development type.

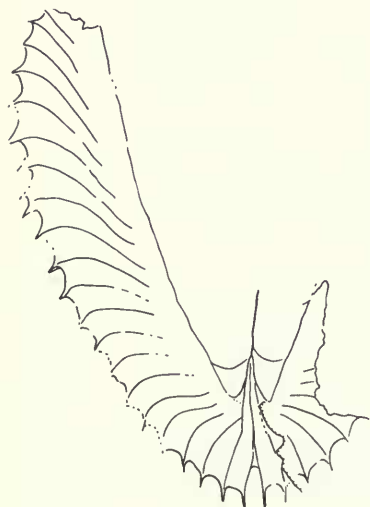


Fig. 57 *Isograptus victoriae maximus* Harris, PMO NF1809, obverse view of incomplete mature rhabdosome; right-hand stipe preserved as impression only. Specimen preserved in relief in limestone, figured by Fortey (1974: text-fig. 6a, b). Basal bed of Profilbekken Member, 145 m above base of Olenidsletta Member; $\times 4$.

With only a single specimen, we cannot rule out the possibility that we have an end member of the *I. victoriae maximodivergens* population instead of *maximus*, since Australasian populations of the two subspecies show considerable overlap (Cooper 1973). However, because the dimensions for sicula length, proximal stipe width and distal stipe width lie so close to the mean values for *I. victoriae maximus*, we refer the Spitsbergen specimen to that subspecies.

Isograptus scandens sp. nov.

Fig. 58a–g; Pl. 5, figs 1–3

DIAGNOSIS. Early *Isograptus* with highly reclined to scandent stipes and highly inclined thecae throughout rhabdosome.

STRATIGRAPHIC RANGE. Olenidsletta Member, V₁c, 49 m from base.

MATERIAL. **Holotype** PMO NF3334; paratypes, PMO NF3335–9, NF3357, NF3379–80 and many other specimens all preserved as flattened casts in black shale.

NAME. 'Scandent.'

DESCRIPTION. The mature rhabdosome has fully scandent stipes whose dorsal margins lie close together, or, in a few specimens, in contact, resulting in a rhabdosome form like that of *Isograptus forcipiformis* or *Skiagraptus*. Stipes are short – up to about 3 mm long – and the rhabdosome has a distinctive ovate outline. Details of the proximal region are obscure in mature rhabdosomes where the distal portion of the sicula commonly appears to be expanded or otherwise modified. Growth stages (Fig. 58a, e, f) clearly show the isograptid symmetry of the sicula and the th1¹, however, and the initial downward growth of proximal thecae. The sicula in the growth stages is 2.75–3.0 mm long and about 0.5 mm wide at the aperture. The supradorsal portion is about 1 mm in length and a short (up to 0.5 mm) nema is present in several specimens. In mature specimens the sicula appears to be slightly longer (3.5 mm) and difficult to distinguish in its distal region from its neighbouring theca (presumably th1²). In one specimen (Fig. 58d) the sicula is short and isograptid symmetry is lost.

In their scandent growth the stipes encroach upon the supradorsal portion of the sicula and th1¹ (Fig. 58b, c, g). Unfortunately, the flattened rhabdosomes do not allow these details of

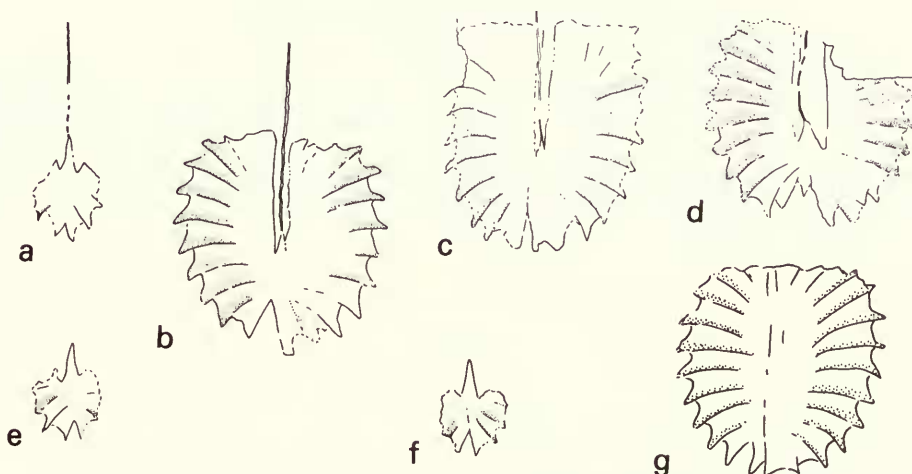


Fig. 58 *Isograptus scandens* sp. nov. All preserved as flattened replaced casts in black shale; all $\times 5$. a, e, f, PMO NF3339, NF3357 and NF3339 respectively; growth stages, showing outline characteristic for growth stages of *Isograptus* species, b, NF3334, **holotype**, best preserved specimen. c, NF3335, large mature rhabdosome, d, NF3336, incomplete mature specimen with sicula possibly inclined and distorted. g, NF3337. All from Olenidsletta Member 49 m above base.

rhabdosome structure to be determined. Stipes reach a maximum width of 2.5 mm in their mid-regions.

Thecae are inclined at a high angle throughout the stipe and are relatively straight. Their ventral margins are commonly enhanced by a thickening of the periderm (i.e. of the replacing mineral) presumably resulting from collapse of the interthecal septum during the flattening of the rhabdosome. There are 8–10 pendent thecae. Thecal apertural margins not deeply recessed.

DISCUSSION. Although most mature rhabdosomes are unmistakably isograptid-like, in several specimens (e.g. Fig. 58d) it is uncertain whether an isograptid or reclined tetragraptid of *T. bigsbyi* type is represented in which the two pairs of stipes are superposed. The distal portion of the sicula is seldom clearly outlined and isograptid symmetry is obscured in some specimens. However, all growth stages show isograptid symmetry and since this feature is not known in any tetragraptid we refer the Spitsbergen form to *Isograptus*. It is assumed that the proximal irregularities affecting the sicula and neighbouring thecae result from either the sicula lying at a somewhat inclined attitude to the median plane of the rhabdosome so as to cause some distortion on flattening or, less probably, that the distal outline of the sicula has been modified by overgrowth (Fig. 58c, g) or resorption (Fig. 58d).

The species is the earliest isograptid in the Spitsbergen sequence where it is confined to the *D. 'protobifidus'* Zone. It is interesting in anticipating the isograptid trend towards scandency; highly reclined or scandent stipes are achieved by other isograptids (e.g. the *manubriatus* and *caduceus* groups) only at much higher stratigraphic levels (Yapeenian). Fusion of the dorsal stipe margins in a specimen such as that of Fig. 58g would result in a rhabdosome of *Skiagraptus* type, at least in outline.

With its highly inclined thecae, the new species differs from all members of the *Isograptus victoriae-caduceus* plexus and instead resembles *Isograptus primulus* Harris from the Chew-tonian of Australasia – that is from the equivalent stratigraphical horizon. The Spitsbergen form is distinguished from the Australasian by its scandent stipes. It is thus thought to belong to a group that is phyletically distinct from the *I. victoriae-caduceus* plexus and the acquisition of isograptid symmetry and scandent stipes in the two groups are therefore examples of convergent evolution.

Genus *PARACARDIOGRAPTUS* Mu & Lee, 1958

TYPE SPECIES. *Paracardiograptus hsui* Mu & Lee 1958.

REMARKS. *Paracardiograptus* is distinguished by the pronounced outward deflection of several pairs of proximal thecae. The overall shape of the rhabdosome is identical with *Cardiograptus* Harris & Keble (*in* Harris 1916) and unless the interthecal grooves or septa of proximal thecae can be seen, the two genera cannot be distinguished. It is likely that *Paracardiograptus* has sometimes been mistaken for *Cardiograptus* and that distribution of the former is not restricted to China, as appears from the literature.

Paracardiograptus? sp.

Fig. 59

1979 *Paracardiograptus?* sp.; Cooper: 73; pl. 14a, fig. 47.

STRATIGRAPHIC RANGE. Profilbekken Member, V₄b, 65 m above base of member, Yapeenian.

MATERIAL. PMO NF3358.

DESCRIPTION AND DISCUSSION. The single fragmentary specimen is preserved as a carbonized, largely flattened rhabdosome in fine-grained calcarenite. Enough of the rhabdosome is preserved to determine that its outline morphology was most probably that of a *Cardiograptus* such as *C. morsus* Harris & Keble (*in* Harris 1916). Further, traces of an early pair of thecae

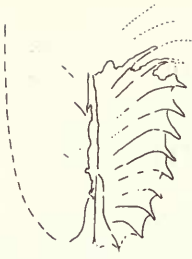


Fig. 59 *Paracardiograptus?* sp. PMO NF3358, fragmentary specimen from Profilbekken Member, V₄b, 65 m above base of member; $\times 4.5$.

(possibly the sicula and th¹₁) can be seen to deflect outwards in their distal region. In this feature and in general outline and proportions the specimen matches that from the Yapeenian of New Zealand described as *Paracardiograptus?* sp. by Cooper (1979).

The outward deflection of proximal thecae is not known in *Cardiograptus*, but is developed to a marked degree in *Paracardiograptus*. The Nelson and Spitsbergen specimens appear to be intermediate between the two genera. Reference of the Spitsbergen species to *Paracardiograptus* is therefore only tentative.

The chief importance of the Spitsbergen specimen lies in its age implications. Neither *Cardiograptus* nor *Paracardiograptus* are known in rocks older than Yapeenian and both *Paracardiograptus* and *Cardiograptus morsus* are confined to that stage. The Profilbekken Member V₄b interval is therefore taken as Yapeenian in part.

Subfamily SIGMAGRAPTINAE nov.

DIAGNOSIS. Sicula relatively long and slender, theca 1¹ originating high on ventral side; first two thecae diverge from sicula more or less at right angles but at different levels, th¹₁ above the level of th¹₂, giving the proximal region an asymmetrical appearance. Prothecal portion of th²₁ extremely slender. Dichotomies of up to 10 or more orders, terminal stipes from 2 to 20 or more. Dichotomies consecutive or delayed, branching progressive or monoprogressive. Thecae long and slender and of low inclination, stipes slender at least in proximal region. Development isograptid, dextral.

DISCUSSION. The distinctive features of Sigmagraptinae are the slender sicula and initial thecae, the uneven levels of divergence from the sicula of th¹₁ and th¹₂ and the extremely slender prothecal portion of th²₁. Thecae throughout the rhabdosome are generally slender, giving the rhabdosome a gracile, commonly rather flexuous appearance, although in some forms thecae and stipes may broaden distally, and in others the proximal region may be thickened by secondary cortical tissue.

The slender prothecal portion of th²₁ can only be seen in isolated relief, or semi-relief, material. It is readily obscured by flattening resulting in a proximal outline with what appears to be *artus* type development. Similarly, subsequent dichotomies employ the normal, isograptid, type of division with a slender 'crossing canal' formed by the prothecal portion of the first daughter theca of the dicalycal theca. Thus development and branching type follow the 'standard' for dichograptoids.

BRANCHING. The branching pattern and number of terminal stipes in the rhabdosome varies widely among the genera here included in the Sigmagraptinae. In *Sigmagraptus*, the initial dichotomy is followed by a succession of dichotomies (up to 10 orders or more) each of which produces one stipe that remains unbranched and a second stipe that undergoes further dichotomy (monoprogressive branching). The resulting characteristic branching pattern is further discussed under *Sigmagraptus*, and we may refer to it as the 'sigmagraptid branching plan'. *Goniograptus* (assuming that we are correct in assigning it to the Sigmagraptinae) undergoes two orders of progressive branching before resorting to the sigmagraptid branching plan and is, in effect, a *Sigmagraptus* based on an initial tetragraptid rather than didymograptid plan.

Where one, two or three 'normal', consecutive dichotomies take place the resulting rhabdosome plan conforms with that of the form genera *Didymograptus*, *Tetragraptus* and *Dichograptus* respectively. There is thus a series of progressive grades parallel to those of the Dichograptinae and, in fact, the three genera above are those into which species with one, two, or three orders of progressive branching have previously been placed. A parallel stipe reduction series has even been proposed (Harris & Thomas 1942) and may well hold true, although supporting stratigraphic data have not yet been described.

However, here the number of terminal stipes is given less stress in phylogeny and classification than the distribution and arrangement of dichotomies (i.e. the branching programme of the rhabdosome), and all the various reduction stages are not given separate names; where generic names are available they have, however, been used. Those sigmagraptines with delayed, and often irregular, dichotomies are separated as a distinct genus, *Laxograptus*, within which the number of terminal stipes is highly variable, both within and between species.

Table 2 Distribution of branching and dichotomy character states among genera of the Sigmagraptinae.

Dichotomy spacing	Branching type and order		
	1 progressive, then many monopressive	2 progressive, then many monopressive	Progressive throughout rhabdosome
Consecutive throughout rhabdosome	<i>Sigmatraptus</i> <i>Trichograptus</i>	<i>Goniograptus</i> <i>Brachiograptus</i>	—
1 & 2 consecutive, later orders consecutive or delayed	—	—	<i>Etagraptus</i>
2nd delayed	<i>Yushanograptus</i>	—	—
2nd and later orders delayed	—	—	<i>Laxograptus</i>
2nd indefinitely delayed	<i>Acrograptus</i>		

GENERA INCLUDED. *Sigmatraptus* Ruedemann 1904, *Trichograptus* Nicholson 1876, *Etagraptus* Ruedemann 1904 (emend.), *Acrograptus* Tzaj 1969 (emend.), and *Laxograptus* gen. nov. (p. 269). Provisionally included are *Goniograptus* M'Coy 1876, *Brachiograptus* Harris & Keble 1932, and *Yushanograptus* Chen, Sun & Han 1964.

The nominate genus includes forms which undergo a single order of progressive branching followed immediately by repeated monopressive branching with only a single normal theca interposed between dicalycal thecae throughout the rhabdosome. Exactly the same branching pattern is followed by *Trichograptus* Nicholson 1876, which differs only in that the lateral stipes are disposed on one side of the main axis, rather than alternately on either side as in *Sigmatraptus*. Examination of the holotype of *T. fragilis* in the BM(NH) revealed a long slender sicula and slender thecae throughout the rhabdosome, and a proximal outline closely similar to that of *Sigmatraptus*. We doubt that the two should be maintained as distinct genera, in which case *Trichograptus* has priority.

Yushanograptus has a similar branching pattern to that of *Sigmatraptus* but several (about 10) normal thecae are interposed between the first and second dicalycal thecae resulting in a

relatively long pair of primary stipes. Its inclusion in the Sigmagraptinae is provisional until details of its proximal structure are clearer.

Goniograptus and *Brachiograptus* each have two orders of progressive branching followed immediately by many orders of monopressive branching. The distinction between them is equivalent to the distinction between *Sigmagraptus* and *Trichograptus* mentioned above and the same reservations about their validity as distinct genera apply. They are only provisionally included in the subfamily until details of their siculae and proximal structure are better known.

Where three orders of progressive branching take place, with interposition of only one normal theca between dicalycal thecae (consecutive dichotomies), the result is a rhabdosome of *Dichograptus* plan. Several slender '*Dichograptus*' species have been described that are likely to be sigmagraptines, including *D. tenuissimus* Harris & Thomas 1942. Similarly, where two orders of progressive branching take place in succession (consecutive dichotomies), the result is a rhabdosome of tetragraptid plan. *Etagraptus* Ruedemann 1904 is a sigmagraptine, as pointed out in our discussion of the form genus *Tetragraptus*, with a rhabdosome of tetragraptid plan. Since the name *Etagraptus* is available, it is here used for the entire group of sigmagraptines with two, three or more orders of progressive branching produced by consecutive dichotomies.

Where only a single, initial, dichotomy takes place the result is a rhabdosome of didymograptid plan. The name *Acrograptus* is available and is here used to denote sigmagraptines with didymograptid rhabdosomes.

Where dichotomies, after the first, are delayed to a greater or lesser extent the result is an irregular rhabdosome for which there is no defined dichograptoid genus available. The name *Laxograptus*, based on *Zygograptus irregularis* Harris & Thomas 1941, is here proposed for such forms. Some of the other species of *Zygograptus* described by Harris & Thomas (1941: 308–310; pls 1, 2) have slender rhabdosomes and may also be sigmagraptines, in which case the range of branching patterns would be further extended. However, until the type species, *Z. abnormis* J. Hall, is better known, the genus *Zygograptus* is best excluded from the Sigmagraptinae.

Genus *SIGMAGRAPTUS* Ruedemann, 1904

[= *Hemigoniograptus* Jin 1977: 81]

TYPE SPECIES. *Sigmagraptus praecursor* Ruedemann 1904.

DIAGNOSIS (revised). Sigmagraptines with one order of progressive branching followed by many orders (up to 10 or more) of monopressive branching, the undivided stipes lying alternately on opposite sides of a main axis formed by the dicalycal thecae. Dichotomies consecutive throughout rhabdosome. Sicula very long and slender, theca 1' originating high on its ventral side. Thecae very slender.

DISCUSSION. The above diagnosis incorporates the new information from the Spitsbergen isolated material. It is now clear that the rhabdosome is essentially half of a *Goniograptus* rhabdosome and apparent anomalies in branching mode have been removed. The term stipe is sometimes used for the main zigzag axes and is convenient but is not strictly correct as they themselves divide at each angulation by a process of normal dichotomous division and each segment should thus be regarded as a separate stipe. Dichotomies thus reach to a high order (10 or more).

The genus contains three species: *S. praecursor* Ruedemann 1904 (= *S. laxus* (T. S. Hall 1914)), *S. crinitus* (T. S. Hall 1914), and *S. yandoitensis* Harris & Thomas 1938. However, it should be noted that if there is more than one theca between branching nodes in *S. yandoitensis* as tentatively suggested by Harris & Thomas, then it would be excluded from the genus *Sigmagraptus* on the above diagnosis. The 'heavy' rhabdosome of *S. crinitus* conflicts with the general rule of slender rhabdosomes in Sigmagraptinae. However, growth stages of *S. crinitus* have not yet been described and it is possible that the thick axial 'stipes' have been produced at a late stage by deposition of secondary cortical tissue as happens in *Clonograptus flexis* (? = *C. rigidus*) described by Braithwaite (1976: 15–19).

Sigmagraptus praecursor Ruedemann 1904

Figs 60a–d, 61a–k

- 1902 *Coenograptid* n.gen. n.sp. Ruedemann: 566.
 1904 *Sigmagraptus praecursor* Ruedemann: 702–703; pl. 5, fig. 13; text-fig. 93.
 1914 *Goniograptus laxus* T. S. Hall: 113, text-fig. 4.
 1935 *Sigmagraptus laxus* (T. S. Hall) Benson & Keble: 272–273; pl. 32, figs 10, 11, ?12.
 1947 *Sigmagraptus praecursor* Ruedemann; Ruedemann: 300; pl. 49, figs 17–20.
 1974 *Sigmagraptus praecursor* Ruedemann; Rickards: 232–239, text-figs 1A–J, 2A–H, 3A–C.
 1979 *Sigmagraptus laxus* (T. S. Hall); Cooper: 57; pl. 49; text-fig. 22.

STRATIGRAPHIC RANGE. Olenidsletta Member, 13–21 m above base, V₁b.

MATERIAL. SM A105799–800, A105802–6, isolated flattened specimens; PMO NF2353, NF2392–3, NF2841, NF2853–4 and several other fragmentary specimens preserved in rock.

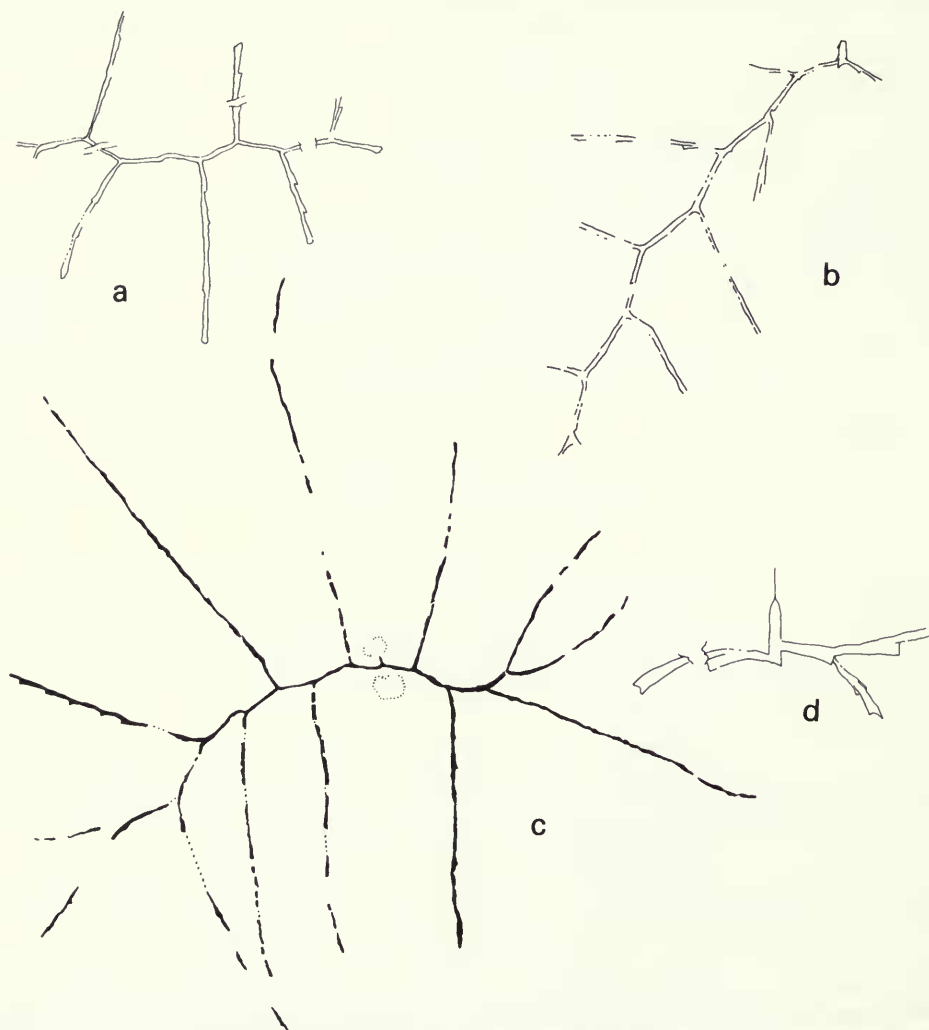


Fig. 60 *Sigmagraptus praecursor* Ruedemann. a, PMO NF2854, incomplete rhabdosome; 18–19 m above base Olenidsletta Member, southern section; $\times 3$. b, NF2393, incomplete mature specimen showing alternate 'lateral' branching; 20–21 m above base Olenidsletta Member, southern section; $\times 3$. c, NYSM 16006, holotype figured by Ruedemann (1904: pl. 5, fig. 13; text-fig. 93), from Bed 3 (*bifidus* Zone) of New York; $\times 3$. d, NF2853, proximal region of specimen in same slab as that of a, showing sigmagraptid asymmetry; $\times 6$.

DESCRIPTION. The rock slab material is fragmentary but sufficient to provide the distinctive features of rhabdosome morphology. Chief interest lies in the isolated material which has yielded several proximal growth stages and branching stipe fragments, and from which initial development and branching mode can be clearly deduced.

Dichotomies up to the 8th order are present in the rock-preserved material and are spaced about 1.8–2 mm in the proximal part of the rhabdosome and 2.2–3 mm in the distal part of the rhabdosome. 'Lateral' stipes reach up to 0.3–0.4 mm in dorsoventral width and some isolated fragments show undulations of the dorsal margin (Fig. 61g, h), not clearly visible in the rock-preserved material. Thecae are spaced approximately 7–9 in 10 mm.

DEVELOPMENT. The sicula is long and slender, measuring 1.1 to 2.0 mm in length and about 0.16–0.19 mm in dorsoventral width at its aperture. The ventral side of the sicula is marked by an extended lip or apertural process. The distal portion of the sicula is deflected towards the stipe² side. Theca 1¹ originates high on the ventral side of the sicula (probably the metasacula), grows down beside it and then curves sharply away from it, leaving 0.1–0.2 mm of the sicular ventral wall free. Theca 1² is given off immediately before the sharp deflection and grows down and across the sicula before turning outward; its ventral margin is approximately aligned with the dorsal margin of the sicular aperture. The first two thecae thus emerge from the sicula at markedly different levels (Fig. 61c, e), giving a characteristically asymmetrical appearance to the proximal end.

Immediately after its origin, th1² gives rise to th2¹ which then grows out as an extremely slender tube along the dorsal side of th1¹. Development is thus of isograptid type and dextral mode. Later development stages were not found.

BRANCHING. An isolated branching stipe fragment (Fig. 61i) shows that the dicalycal theca (n) arises from th(n – 1) at the level of the aperture of the previous theca (n – 2). The dicalycal theca grows away from its parent theca to form one branch and gives off its first daughter theca almost immediately which in turn follows the parent theca (n – 1) to give rise to the second branch. Branching mode is thus of isograptid type. In relating the isolated branching fragment to the rhabdosome, two interpretations are possible. The dicalycal theca may comprise the main zigzag stipe (Fig. 61j) or it may form the basal theca of the lateral branch (Fig. 61k). Because there is no evidence of a second branching node at the level of the aperture of theca (n + 1) as would be expected in the second interpretation above, the first interpretation is favoured here. Of the two it is the one consistent with Rickards' (1974: fig. 2F) figure showing the dicalycal theca producing its daughter theca about halfway between branching nodes as a 'distinct lump'. The dicalycal theca is thus 'free' in its mid region, and the main 'stipe', at this point, is composed of but a single theca. In the alternative view (Fig. 61k) the main stipe is comprised of two adjacent but not successive thecae at any given point. In either case, each dicalycal theca alternates with a normal unicalycal theca.

The interpretation preferred here is consistent with branch structure in *Goniograptus* described by Jaanusson (1965) but conflicts with that described by Rickards (1974; see discussion below) in *Sigmagraptus praecursor*. It also indicates that 'lateral' branch formation does not differ fundamentally from dichotomous stipe division.

OVERALL DEVELOPMENT PLAN. A model for the overall thecal budding plan of the rhabdosome can thus be proposed and is shown in Fig. 62. The main zigzag axes or 'stipes' are composed of dicalycal thecae and the unbranched 'lateral' stipes develop from the first of the two daughter thecae of each dicalycal theca. Throughout the rhabdosome, dichotomies are consecutive and dicalycal thecae are separated, in budding sequence, by a single normal (unicalycal) theca.

DISCUSSION. The species is commonly found in great profusion, forming dense mats on the bedding plane. One specimen (NF2853, Fig. 60d) shows the distinctive asymmetrical proximal end, otherwise known only from isolated material. Length of the sicula is variable in the Spitsbergen material but generally is less than 1.5 mm.

Ruedemann's figures (1904: pl. 5, fig. 13; text-fig. 93) of the holotype from Bed 3 (*bifidus* Zone) of New York show an improbably long sicula, at least 5 mm long. The specimen has.

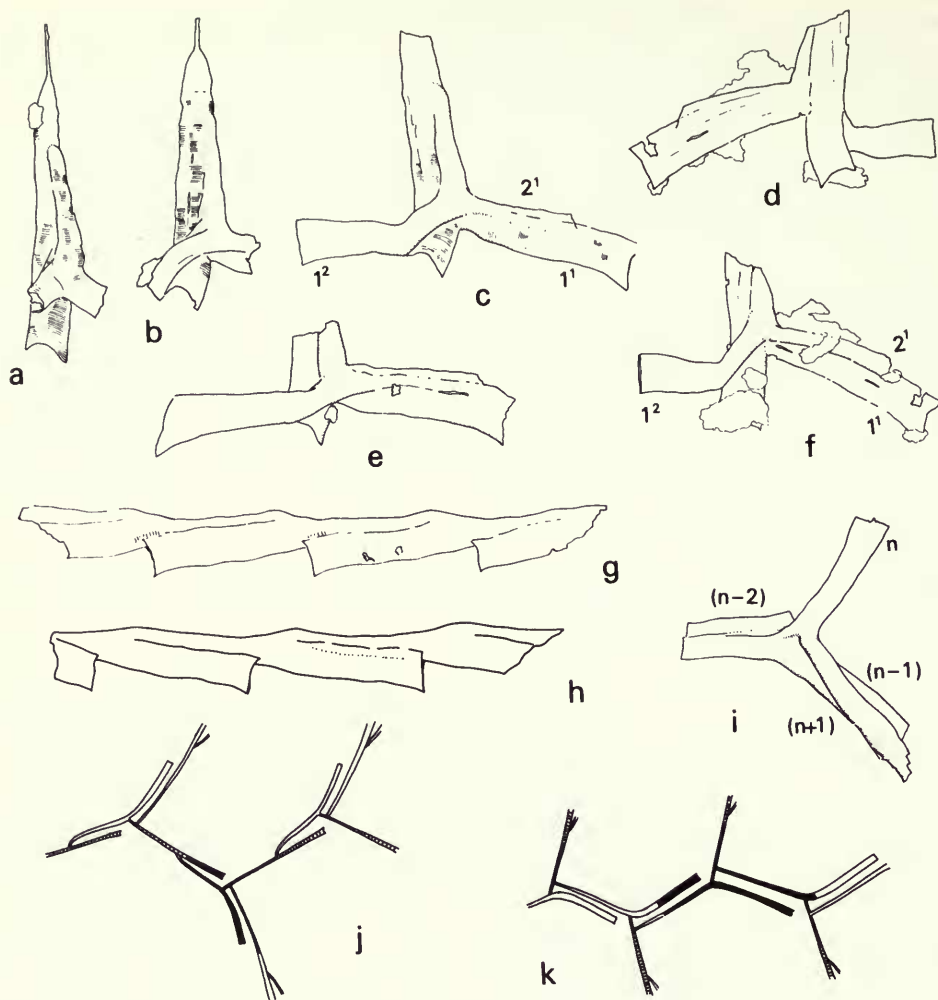


Fig. 61 *Sigmagraptus praecursor* Ruedemann, isolated specimens from Spitsbergen. a, SM A105806, early growth stage showing origin of $th1^1$ on, probably, metasicula and ventral apertural extension of sicula. From 17–18 m level; $\times 30$. b, SM A105802, incomplete later stage, isograptid arch formed. From 16–17 m level; $\times 30$. c, SM A105800, stage in which $th2^1$ has grown part way along the dorsal margin of $th1^1$ as a slender tube, isograptid development clear. From 16–17 m level; $\times 30$. e, SMA105799, incomplete growth stage similar to that of c. From 16–17 m level; $\times 30$. g, h, SM A105805 and SM A105804 respectively, stipe fragments showing weakly-developed prothecal folds. g from 17–18 m level, h from 16–17 m level; $\times 20$. i, SM A105803, fragment of branching stipe from 16–17 m level on which thecal diagrams shown in Fig. 61j (preferred here) and Fig. 61k have been based; $\times 30$. d, f, SM A105807, sigmagraptine growth stage possibly referable to *S. praecursor* in which the sicula protrudes below the level of $th1^1$ and in which isograptid development is clearly displayed. From 16–17 m level; $\times 30$. All from Olenidsletta Member, type section.

been re-examined and is refigured in Fig. 60c. There is no trace of the structure figured by Ruedemann but the shale matrix has been excavated at two places, one above and one below the median axis of the rhabdosome. The apex of a longer sicula could have been removed by one excavation, but the other lies clear of the ventral rhabdosome margin and there is no sign of a projection of the sicula below the ventral rhabdosome margin as would be expected from

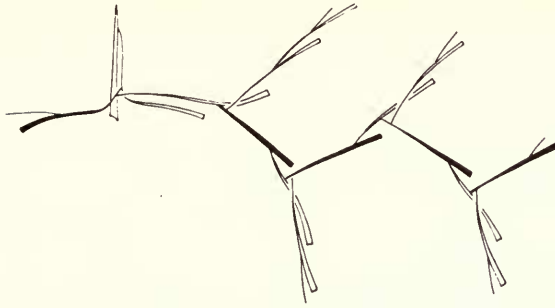


Fig. 62 *Sigmagraptus praecursor* Ruedemann. Thecal diagram to show our inferred overall thecal budding plan of the rhabdosome. Dicalycal thecae shown in solid black. Proximal development is of isograptid type and dextral mode and all subsequent dichotomies employ isograptid division; successive dicalycal thecae are separated by unicalycal thecae.

Ruedemann's figure. It is assumed that the original figure incorporated a misinterpretation of the sicula. The Spitsbergen material matches the refigured holotype and Ruedemann's description well except in having a somewhat wider spacing of dichotomies in the distal part of the rhabdosome.

Rickards (1974) described a population of flattened and pyritized rock-preserved material of *S. praecursor* from the Levis Shales at localities attributed to Zone C. Associated forms include *D. bifidus* (a Zone C form), and *Tetragraptus fruticosus* suggesting that Zone B may also be represented. He interpreted initial development as of *artus* (= '*bifidus*' type). In describing the mode of branching Rickards (1974: 236) interpreted the basal theca of the branch as arising directly from what he interpreted as the dicalycal theca of the 'main stipe'. Branching mode would thus be of *artus* type (and unique) and the 'main stipe' was therefore thought to be composed of a succession of dicalycal thecae with no intervening unicalycal thecae, differing from that of *Goniograptus* (Jaanusson 1965) in which the dicalycal thecae alternate with normal unicalycal thecae.

The isolated Spitsbergen material described here, however, clearly shows that both initial development and branch structure are of isograptid type. Some of the isolated proximal ends, on the other hand, are flattened to the extent that the initial slender part of th2¹ cannot be discerned and the 'isograptid arch' is obscured. Such specimens have the appearance of possessing *artus* type development, as drawn by Rickards, but there is little doubt as to their true mode of development and they emphasize the importance of well-preserved material for the interpretation of development and structure of slender dichograptoids. Similarly the intricate isograptid branch structure is apparent only in our well-preserved isolated material. It seems likely that these fine details of structure were not preserved in Rickards' material. No structures equivalent to the peculiar pseudovirgulae described by Rickards are present in our material, but the appropriate growth stages may not be represented.

The form referred by Australasian workers (Benson & Keble 1935; Cooper 1979) to *Sigmagraptus laxus* (T. S. Hall 1914) is here thought to be synonymous with *S. praecursor* Ruedemann. Hall's description is extremely brief but is consistent with Ruedemann's species and his figure shows only generalized rhabdosome form. Hall did not comment on the distinction of *laxus* from *praecursor* and there seems insufficient reason for maintaining it as a distinct species.

Sigmagraptus (?) *crinitus* (T. S. Hall 1914)

Pl. 2, fig. 4

?1914 *Goniograptus crinitus* Hall: 111–112, text-figs 2, 3.

STRATIGRAPHIC RANGE. Lower Olenidsletta Member 13 m from base, in Late Bendigonian (early Arenig) fauna.

MATERIAL. One nearly complete rhabdosome, SM A105819.

DISCUSSION. The determination given here is based on the good specimen of *G. crinitus* from Victoria illustrated by Harris & Thomas (1939: fig. 14); the specimen from Spitsbergen is not well enough preserved to show thecal details. This is a very robust *Sigmagraptus* species compared with *S. praecursor*, which is the common form in our collections. The two zigzag main stipes are much thicker than the laterals, and they appear to curve gently upwards distally. Lateral branches are spaced about 3 mm apart on the same side of each primary stipe; initially they are straight and rigid, but distally they become bent or twisted, suggesting that they were originally quite flexible. Some of these slender laterals certainly exceeded 4 cm in length. *S. crinitus* is a rather distinctive species, and this is its first record outside Bendigo, Victoria.

The sigmagraptine affinity of the species is not apparent from either our material or from the Victorian specimen. Details of proximal structure cannot be seen in specimens from either region, and the nature of the heavily thickened zigzag stipe and arrangement of thecae along it are similarly unknown. Until these details are clarified the species is only provisionally included within the genus.

Genus *GONIOGRAPTUS* M'Coy, 1876

TYPE SPECIES. *Didymograpsus thureaui* M'Coy 1876.

Goniograptus thureaui (M'Coy 1876)

Pl. 3, fig. 1

1876 *Didymograpsus thureaui* M'Coy: 128–130, one fig.

1904 *Goniograptus thureaui* (M'Coy); Ruedemann: 621–624, text-figs 37–38; pl. 6, figs 1–15.

1939 *Goniograptus thureaui* (M'Coy); Harris & Thomas: 55, figs 1a–b.

1979 *Goniograptus thureaui* (M'Coy); Cooper: 56; pl. 5d.

STRATIGRAPHIC RANGE. Lower part of the Olenidsletta Member (early Arenig, late Bendigonian); associated trilobite fragments indicate about 4 m from base.

MATERIAL. A single incomplete specimen. SM A105820.

DISCUSSION. The only specimen of this species was found loose on Olenidsletta, but there is no doubt that it came from the lower (Bendigonian) part of the Olenidsletta Member. The proximal end is not preserved, but three of the four stipes are visible, and there is no question of its reference to *Goniograptus*. There appear to have been three or four branches on each side of the four major stipes, and the half rhabdosome preserved suggests that the whole specimen would have had 24–26 branches. This is somewhat less than typical specimens from Bendigo, Victoria (Harris & Thomas 1939) and New Zealand (Cooper 1979). It is like the forms that Ruedemann (1904) termed var. *postremus* and Harris & Thomas (1939) var. *inequalis*. Only two species of *Goniograptus* are like our form: *G. thureaui* and *G. speciosus* T. S. Hall. The latter has much thicker and longer stipes than our specimen, and the proportions, and what thecal details there are, agree closely with descriptions of *D. thureaui* in Ruedemann (1947) and Cooper (1979). The 'varieties' recognized by Harris & Thomas (1939) and Ruedemann (1904) are probably no more than intraspecific variants, with relatively fewer branches.

Genus *ETAGRAPTUS* Ruedemann, 1904, emend.

TYPE SPECIES. *Etagraptus lentus* Ruedemann 1904.

DIAGNOSIS (revised). Sigmagraptines with stipes of two, three or more orders in which dichotomies of the first two orders are consecutive. Branching of progressive type.

SPECIES. *Etagraptus lentus* Ruedemann 1904, *Dichograptus tenuissimus* Harris & Thomas 1942, (?) *Bryograptus pusillus* Ruedemann 1904 and (?) *Tetragraptus harti* T. S. Hall 1914.

DISCUSSION. The dicalycal thecae of the first two dichotomies are separated by a single normal theca resulting in an initial development of the rhabdosome following the tetragraptid plan. The third dichotomy, if present, follows the second with one or more intervening normal thecae; in those rhabdosomes with only one intervening normal theca, e.g. in '*Dichograptus*' *tenuissimus*, the rhabdosome plan follows that of *Dichograptus*. In *Bryograptus pusillus* the third and subsequent dichotomies are somewhat delayed. *B. pusillus* departs from a general pattern among sigmagraptines in having pendent rather than horizontal first-order stipes and is therefore only tentatively included here. It seems best, however, to leave the generic diagnosis sufficiently broad to receive such forms.

Ruedemann's (1947: 312) diagnosis of *Etagraptus* incorporated *Tetragraptus approximatus* and laid emphasis on the H-shape of the rhabdosome. We emphasize the sigmagraptine character of the rhabdosome and regard the number and attitude of stipes as of secondary importance.

Several of the Arenig species now usually classified under the 'umbrella-name' *Clonograptus* are likely to belong here.

Etagraptus tenuissimus (Harris & Thomas 1942)

Fig. 63a

1942 *Dichograptus tenuissimus* Harris & Thomas: 366; pl. 1, figs 3, 3a.

STRATIGRAPHIC RANGE. Olenidsletta Member, 18–19 m above base, V₁b.

MATERIAL. PMO NF2814 and other incomplete rhabdosomes in the same slab.

DESCRIPTION. Rhabdosome of *Dichograptus* grade with three orders of consecutive branching. Sicula morphology and proximal structure unknown. First-order stipes together are 2.4 mm long and appear to be comprised of a single theca each. Second-order stipes are also composed of a single theca each and are 1.0–1.2 mm long. Third-order stipes are at least 6.5 mm long and have a slight dorsal undulation. Stipes of first and second orders are about 0.2 mm in lateral width, those of the third order reach 0.4 mm in dorsoventral width. Thecae are long and slender and inclined at less than 20°. They are spaced 4 in 5 mm (= 8 in 10 mm).

DISCUSSION. Harris & Thomas (1942: 366) claimed that the closest relatives of this slender dichograptoid of *Dichograptus* grade lie not within the genus *Dichograptus* but in other

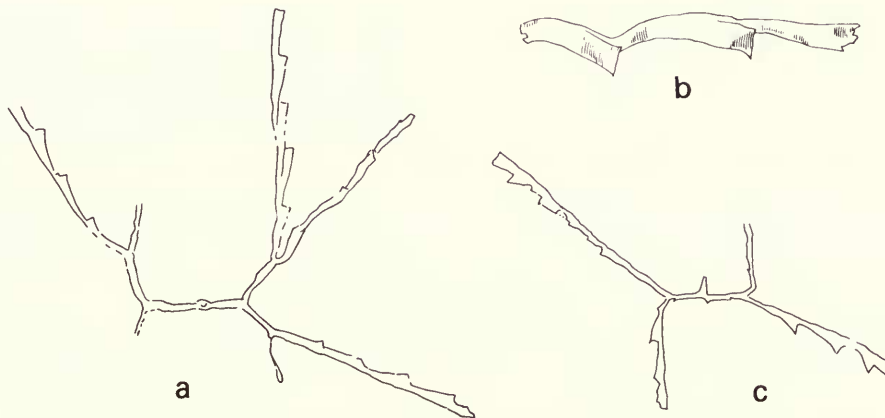


Fig. 63 a, *Etagraptus tenuissimus* (Harris & Thomas), PMO NF2814, incomplete mature rhabdosome from 18–19 m above base of Olenidsletta Member, southern section; $\times 5$. b, SM A105808, fragment of stipe possibly attributable to *E. tenuissimus*, 16–17 m above base of Olenidsletta Member, $\times 20$. c, *Etagraptus* sp. indet., PMO NF2803; incomplete rhabdosome from 25 m above base of Olenidsletta Member, southern section; $\times 3$.

'genera' such as *Goniograptus* (*G. macer*), '*Tetragraptus*' (*T. harti*), '*Didymograptus*' (*D. gracilis*), etc. In other words they took as a key character thecal type rather than number of stipes (or dichotomies).

Our observations on the admittedly imperfect Spitsbergen material fully support the conclusions of Harris & Thomas. We therefore group this species with other slender species with similar thecae – in the Sigmagraptinae. Unfortunately, sicular morphology and proximal structure are unknown and the assignment must remain provisional.

Etagraptus harti (T. S. Hall 1914)

Fig. 64

- 1914 *Tetragraptus harti* T. S. Hall: 113–114, text-figs 5–6.
 1938 *Tetragraptus harti* Hall; Harris & Thomas: 73; pl. 2, figs 14a–b; pl. 4, fig. 13.
 ?1964 *Tetragraptus zhejiangensis* Ge: 393–394; pl. 1, figs 1–8.
 1979 *Tetragraptus harti* Hall; Cooper: 65; pl. 7f, fig. 33.

STRATIGRAPHIC RANGE. Olenidsletta Member, 18–19 m above base, V₁b.

MATERIAL. PMO NF2854, and several immature rhabdosomes.

DESCRIPTION. Rhabdosome horizontal. Details of sicula and early development unknown. First-order stipes appear to be composed of a single theca each and together form a 'funicle' 2.5 mm long. Second-order stipes are straight, rigidly diverging, and slender reaching a maximum width of 0.5 mm at the 7th theca. Length of second-order stipes reaches 14 mm but isolated stipe fragments possibly attributable to the species are considerably longer. Thecae are of low inclination and in some views appear to be slightly sigmoidal, with a gently undulating dorsal stipe margin. They are spaced 7 in 10 mm (6 in 8.5 mm).

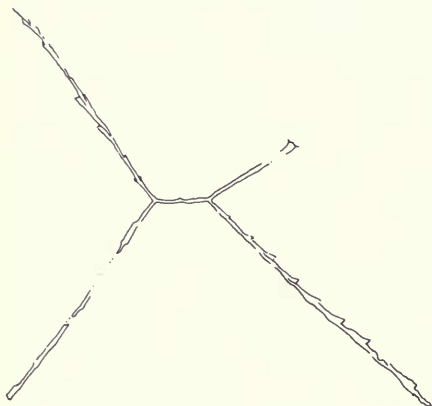


Fig. 64 *Etagraptus harti* (T. S. Hall), PMO NF2854, incomplete mature rhabdosome with second-order stipes showing gentle dorsal undulations; 18–19 m above base of Olenidsletta Member, southern section; $\times 3$.

DISCUSSION. Although only a single specimen has been referred to *E. harti*, the species is likely to be more abundant in our collections. Several bedding planes at about the 18–19 m level are littered with stipe fragments or superposed specimens that are insufficiently clear to be assignable to a species but some of which probably represent *E. harti*.

Hall's species is not particularly well characterized but the Spitsbergen material is obviously similar in gross rhabdosome dimensions and in general thecal characters. Hall's specimens come from the Bendigonian of Victoria, a similar horizon to that of the Spitsbergen specimens.

The species is distinguished from other quadriramous dichograptoids by the extreme tenuity and rigid divergence of its stipes. *Etagraptus lentus* Ruedemann has somewhat lax second-order stipes and the rhabdosome has an H-shape. *Tetragraptus quadibrachiatus* has a similar rhabdosome shape but heavier stipes and more highly inclined thecae. *Tetragraptus zhejiangensis* is closely similar but comes from a considerably higher horizon and appears to have slightly dependent second-order stipes (Ge 1964: pl. 1, figs 5, 6).

Harris & Thomas (1942) have suggested that *E. harti* forms part of a lineage including *Goniograptus macer*, '*Dichograptus*' *tenuissimus* and '*Didymograptus*' *gracilis*. The slender stipes with widely spaced thecae of low inclination certainly strongly suggest that it belongs (along with the above species) in the Sigmagraptinae. The species is therefore here referred to the genus *Etagraptus* although until details of sicular morphology and proximal structure are known, the assignment must remain provisional.

Genus *LAXOGRAPTUS* nov.

TYPE SPECIES. *Zygograptus irregularis* Harris & Thomas 1941.

DIAGNOSIS. Sigmagraptines with stipes of two or more orders in which dichotomies after the first are delayed and somewhat irregular. Branching is generally of progressive type; rhabdosome of lax habit.

NAME. *Laxus*, 'loose,' referring to the branching habit.

SPECIES. *Zygograptus irregularis* Harris & Thomas 1941, *Bryograptus lapworthi* Ruedemann 1902, *Tetragraptus whitelawi* T. S. Hall 1914, and (?) *Dichograptus sedecimus* Harris & Thomas 1938.

DISCUSSION. The initial dichotomy produces a pair of relatively long first order stipes. It is followed by further dichotomies at delayed and somewhat irregular intervals producing branching of generally progressive type of up to four, five or even more orders. The irregular spacing of dichotomies appears to be variable from one rhabdosome to another, and within single rhabdosomes. In this respect they depart conspicuously from the general rule of regularity and symmetry in rhabdosome development in the Graptoloidea, and recall the irregularity and 'instability' in development of many dendroids, particularly *Adelograptus* and *Bryograptus*.

The first dichotomy and, indeed, the development of the proximal region as far as it can be determined, is of normal sigmagraptine type. The second dichotomy takes place after several thecae of the first-order stipes have been formed. In *L. irregularis* the first-order stipes can be of different lengths (Harris & Thomas 1941: 310) and bear up to 10 or more thecae. The number of thecae in stipes of later orders again is variable within and between specimens. In *L. irregularis* some second-order stipes fail to divide at all. Where dichotomies after the first are relatively closely spaced, the rhabdosome form approaches that of *Zygograptus* Harris & Thomas.

In specimens of *L. irregularis* from New Zealand, figured by Cooper (1979: pl. 3f) the postponement of dichotomy, after the first, is extremely marked. The longer of the two first-order stipes contains at least 21 thecae and second-order stipes contain 16 or more thecae. Incomplete growth stages of these rhabdosomes are indistinguishable from *Acrograptus* which could easily be produced by indefinite delay of the second dichotomy. If dichotomies after the second were indefinitely delayed the result would be a rhabdosome like that of *Tetragraptus whitelawi* T. S. Hall.

The significance of the denticulate apertural extensions in *Dichograptus sedecimus* (Harris & Thomas 1938) is uncertain. Whereas such a thecal character would be expected to carry taxonomic significance at a fairly high level, the feature is shown by several species of different genera from the same locality – the 'Good Bed' of Campbelltown, Victoria – leading to the suggestion that it might be environmentally induced, and hence of limited taxonomic value. The species is therefore tentatively included here.

Some of the Arenig *Clonograptus* species, such as *C. ramulosus* Harris & Thomas 1938 and *C. rarus* Harris & Thomas 1938, with slender flexuous rhabdosomes and delayed branching, might well belong in *Laxograptus*.

Laxograptus irregularis (Harris & Thomas 1941)

Fig. 65a–d; Pl. 4, fig. 1

1941 *Zygograptus irregularis* Harris & Thomas: 310; pl. 1, figs 7–9; pl. 2, fig. 5.

1979 *Zygograptus irregularis* Harris & Thomas; Cooper: 57–58; pl. 3f.

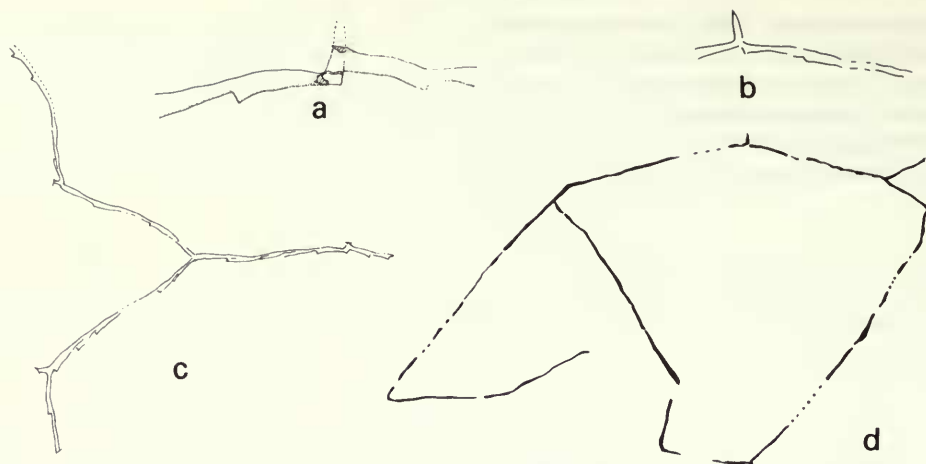


Fig. 65 *Laxograptus irregularis* (Harris & Thomas). a, PMO NF3330a, proximal region showing different levels of divergence of initial two thecae from sicula; 16–17 m above base of Olenidsletta Member, type section; $\times 12$. b, d, NF658, enlarged proximal region ($\times 5$) and incomplete mature rhabdosome ($\times 2$). Note asymmetry in first-order stipe length. 54 m above base of Olenidsletta Member, type section. c, NF3330b, incomplete specimen with 3 orders of dichotomy. Same slab as a; $\times 4$.

STRATIGRAPHIC RANGE. Olenidsletta Member, 16–54 m above base, V_1b and V_1c .

MATERIAL. PMO NF658 and NF622 (counterparts), NF3330, SM A105807 (?) and numerous fragments.

DESCRIPTION. Rhabdosome of lax habit and at least three orders of slender flexuous stipes. Sicula relatively long and slender, proximal region of sigmagraptine type with the two initial stipes diverging from the sicula at different levels. Proximal development is unknown but the similarity of the proximal outline to that of *Sigmatraptus praecursor* suggests that proximal structure in the two forms is similar. First-order stipes with five or more thecae, varying in length from rhabdosome to rhabdosome; together they form a more or less straight 'funicle'. Second-order stipes with six or more thecae, again varying in length from rhabdosome to rhabdosome. Third-order stipes are up to 300 mm long. Detailed morphology of thecae unknown, but they appear to be similar to those of *Sigmatraptus praecursor*. Thecal spacing unknown.

DISCUSSION. The main features of the species have already been discussed. Harris & Thomas's (1941) figures give no details of sicula or thecal morphology other than that thecae are slender and of *Sigmatraptus praecursor* type. The species is found in the Chewtonian and Castlemainian (Ca 1) in Australasia and in the Chewtonian and late Bendigonian of Spitsbergen. Ruedemann's (1902) species *Bryograptus lapworthi*, from Beds 1 and 2 of the Deep Kill section of New York (i.e. in strata equivalent to Bendigonian and Chewtonian age), has a similar irregular rhabdosome form and may well prove to be a senior synonym of *L. irregularis*.

Genus *ACROGRAPTUS* Tzaj, 1969

TYPE SPECIES. *Didymograptus affinis* Nicholson 1869.

EMENDED DIAGNOSIS. Sigmagraptines with stipes of two orders; stipes horizontal to deeply declined, narrow at the proximal end, 0.5 mm wide or less.

DISCUSSION. As originally proposed, *Acrograptus* was an upgrading of Elles & Wood's (1901) informal division of *Didymograptus* species with a declined rhabdosome habit. We do not regard the habit as particularly important; this is shown by the very close resemblance between

such species as *Didymograptus filiformis* Tullberg 1880 with declined habit, and *D. gracilis* Törnquist 1890, a normal extensiform, which it would be absurd to place in different genera on the basis of stipe habit alone. However, the structure of the proximal end of the type species of *Acrograptus* shows (Fig. 66a) the long slender sicula, and the proximal siting of $th1^1$ and $th1^2$ at different levels on the sicula which we describe here as typical of *Sigmagraptus* and allied forms. There is a group of didymograptid species which show the same structure (e.g. Bouček 1973: pl. 11, figs 2, 5; Mu *et al.* 1979: pl. 27, fig. 13), and it is this character which in our opinion distinguishes *Acrograptus* from other Arenig didymograptids, regardless of overall rhabdosome form. Since the proximal end structure resembles that of *Sigmagraptus*, but differs from that of *Didymograptus* (*Expansograptus*) or *Didymograptus* (*Didymograptellus*), it is concluded that *Acrograptus* is more closely related to the *Sigmagraptus*–*Goniograptus* group than to other species with didymograptid habit. Hence it should be included as a separate genus within the Sigmagraptinae rather than as another subgeneric division of *Didymograptus*.

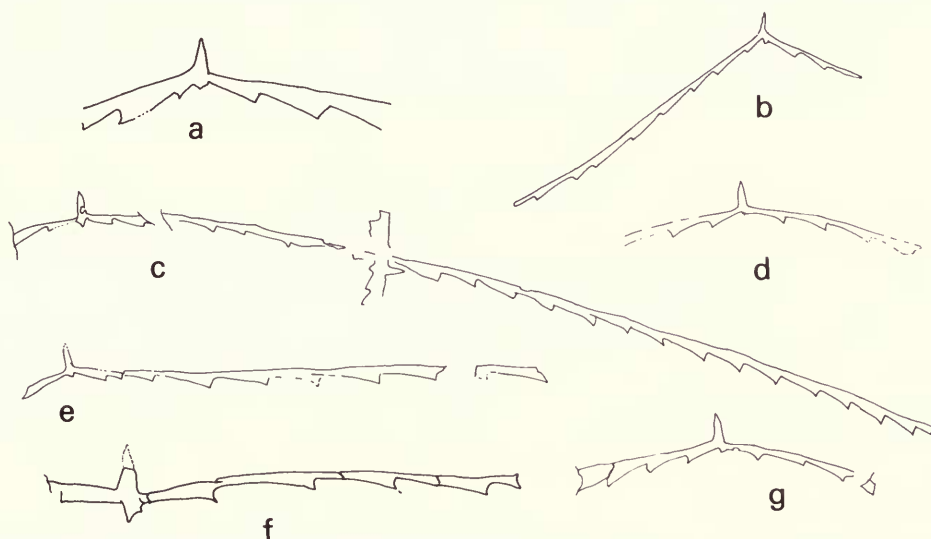


Fig. 66a *Acrograptus affinis* (Nicholson). Holotype, BM(NH) Q3108, proximal end; the original of Nicholson (1869: pl. 11, fig. 20). Skiddaw Slates, $\times 10$.

Fig. 66b *A. cf. affinis*. PMO NF654, 60 m above base of Olenidsletta Member on Profilstranda; $\times 4$.

Fig. 66c–g *Acrograptus gracilis* (Törnquist). c, NF824, large specimen from 35 m above base of Olenidsletta Member on Profilstranda; $\times 4$. d, e, NF3329 and NF3328 respectively, 49 m above base of Olenidsletta Member, southern section; $\times 5$. f, Lund University LO923-6t, specimen from the type slab of Törnquist (1890); $\times 10$. g, NF3329, proximal portion, same horizon as c; $\times 5$.

As far as development type is concerned, the well-preserved species *A. lipoldi* described by Bouček (1973) clearly shows isograptid development, which we would expect by comparison with *Sigmagraptus*. The asymmetry of the proximal end may be partly the result of the broader crossing canal connected with the isograptid development type. Bouček interprets another *Acrograptus* (*A. nicholsoni*) as probably having *artus* development. As we have shown elsewhere, this can be very difficult to interpret from flattened material. However, Bulman (1936a: 27) also suggested *artus* development for a Llanvirn species similar in most respects to typical Arenig *Acrograptus*, although he comments that the isolated material is not well-preserved. Skevington (1965) indicated a similar development for a species identical to that of Bulman, although again preservation was imperfect. The initiation of $th1^1$ is also lower on the sicula than in typical Arenig species. If *artus* development is confirmed for the younger material it seems that there are two possibilities: either these younger species were derived from *Didymograptus* (*Didymograptus*) with the same kind of development, or (and we consider this more likely) the same kind of reduction of $th1^2$ occurred in the sigmagraptine lineage that we have proposed in the pendent didymograptid group.

Acrograptus gracilis (Törnquist 1890)

Fig. 66c–g

1890 *Didymograptus gracilis* Törnquist: 17; pl. 1, figs 9–12.

STRATIGRAPHIC RANGE. Olenidsletta Member, 35 m to 55 m from base, V_1 b–c, Arenig, *Didymograptus protobifidus* Zone.

MATERIAL. PMO NF824, NF3328–9, NF3342.

DESCRIPTION. Sicula 1·0–1·1 mm long, and very slender. Theca 1^1 and $th1^2$ grow out normal to axis of sicula, and at different levels, $th1^1$ being the higher of the two. Small growth stages are rather common along with *Isograptus scandens* sp. nov. in the dark silt at 55 m above the base of the Olenidsletta Member on Olenidsletta, where they present a distinctive, lop-sided appearance because of the growth of the first two thecae, as shown by Törnquist (1980: pl. 1, fig. 12). The initial growth of the stipes is horizontal, or very nearly so, but distally they may be gently declined, and it is not unusual to find portions of stipes probably belonging to this species preserved twisted in such a way as to suggest that they were originally quite flexible. Our best specimen has one stipe 3 cm long. Lengths of free ventral walls of $th1^1$ and $th1^2$ are 1 mm, and all the thecae along the stipe are similarly long and narrow (free ventral walls up to 1·3 mm) and inclined at an extremely low angle. Stipe width at $th1^1$ is 0·2–0·3 mm and there is a very gradual increase in width of stipes to a maximum of 0·5 mm distally. When a true thecal profile is preserved it is clear that the thecae were flared at the aperture, to generate a slightly acute angle between ventral wall and apertural margin. Distal thecal spacing is 7 in 10 mm.

DISCUSSION. The important character of this species, as Törnquist originally specified, is the horizontal direction of the first two thecae. Our specimens compare closely with the types, which we have examined; although the Spitsbergen examples attain a slightly greater stipe width they are also longer than Törnquist's types. *Didymograptus ellesae* Ruedemann (1904) seems to have a similar habit to that of our largest specimen, with distal declination of the slender stipes. The thecal spacing of this species is stated to be 10–12 in 10 mm, and it is outside the range of *A. gracilis* in this regard.

Acrograptus cf. *affinis* (Nicholson 1869)

Fig. 66b

cf. 1869 *Didymograptus affinis* Nicholson: 240; pl. 11, fig. 20.

STRATIGRAPHIC RANGE. Olenidsletta Member, 60 m from base.

MATERIAL. PMO NF654.

DISCUSSION. A single specimen from above the range of *A. gracilis* has distinctly declined initial thecae (enclosing an angle of about 120°) and cannot therefore be included in that species. Like *A. gracilis* the thecae are long and narrow, and the stipes are only about 0·4 mm wide distally. Examination of the specimens of *A. affinis* figured by Elles & Wood (1901; including the type) shows similar proportions at a comparable stage of growth, although the specimen figured on their pl. 2, fig. 1a has closely spaced theca, 12 in 10 mm. Bouček's (1973) revision of *A. nicholsoni* shows that this species can include individuals close to *A. affinis*, although distal stipe width is apparently greater in *A. nicholsoni*. Comparative work on populations from the type localities of *A. affinis* and *A. nicholsoni* is needed to clarify the acceptable range of variation of these species. We compare our specimen with *A. affinis* because of its slender stipes.

Family PHYLLOGRAPTIDAE Lapworth 1873, emend.

DIAGNOSIS. Development platycalcal, of isograptid type and dextral mode. Virgellar spine present, theca 1^1 originates and develops on antivirgellar (dorsal) side of sicula. Rhabdosome bilaterally symmetrical, composed of two or four stipes, horizontal to scandent.

DISCUSSION. Lapworth's (1873) family Phyllograptidae is here revived to include forms with a virgellar spine on the sicula. All such forms differ fundamentally from the bulk of dichograptoids in their earliest development – th1' originates and develops on the antivirgellar (dorsal) side of the rhabdosome rather than on the virgellar (ventral) side. Subsequent development follows the 'orthodox' dichograptoid pattern and is of isograptid, platycalycal, type and dextral mode.

The family, as known at present, comprises two genera, *Phyllograptus* Hall *sensu stricto*, and *Xiphograptus* gen. nov. based on *Didymograptus formosus* Bulman. In both genera, the sicula is relatively short, about 1.5 mm or less in length, and similar in morphology. The two genera, however, differ markedly in morphology of the rhabdosome and their close relationship is apparent only when details of the sicula and earliest development are taken into account. Fortunately, although these features can be clearly seen only in isolated material, the presence of a virgellar spine can usually be determined in flattened material providing preservation is reasonably good as, for example, in *Didymograptus formosus svalbardensis*, discussed below. As details of sicular morphology and earliest development of dichograptoids become more widely known, we think it likely further species will be found to possess virgellar spines and the range of rhabdosome types within the Phyllograptidae will expand.

Genus *PHYLLOGRAPTUS* Hall, 1858

TYPE SPECIES. *Phyllograptus typus* Hall 1858.

REVISED DIAGNOSIS. Quadriserial, scandent rhabdosome with four stipes united along their dorsal margins; median septa separating adjacent thecal series reduced to a framework of fornice and a central columella with an open foramen between thecae of adjacent series. Initial thecae distally reclined.

DISCUSSION. The new information on development and structure revealed by the Spitsbergen material shows that *P. typus* is radically different from phyllograptids of the *angustifolius* group and should be placed in a separate genus. Since it is the type species of the genus *Phyllograptus* Hall, by original designation, phyllograptoids with development and structure of *angustifolius* type (fully described by Holm 1895, Bulman 1936a and Skevington 1965) must be transferred to a new genus, for which the name *Pseudophyllograptus* is proposed (p. 241). It is unfortunate that the concept of the genus *Phyllograptus* has, until now, been based largely on the isolated material of *angustifolius* mentioned above.

Since distinction between the two genera is based primarily on features seen only in relief material, a particular problem is posed in trying to assess the affinity of previously described 'phyllograptoids', almost all of which are based on flattened material. The presence of a columella and fornical foramina can sometimes be inferred in flattened specimens (e.g. Mu *et al.* 1979: pl. 42, fig. 6; pl. 43, figs 18, 19) as can the reclined growth of proximal thecae and the initially low angle of inclination of subsequent thecae. The somewhat pointed proximal rhabdosome outline and sicular (virgellar) spine of *Phyllograptus*, *sensu stricto*, can usually be determined. The sicular spine, which is prominent in the Spitsbergen growth stages, has to be looked for carefully in mature rhabdosomes. It is, of course, a greatly enlarged feature in Hall's type material from Levis and its importance lies not in its size but in its presence.

SPECIES. *Phyllograptus typus* Hall 1858, *P. anna* Hall 1865, *P. ilicifolius* Hall 1858, *P. uniformis* Ge (in Mu *et al.* 1979) and *P. acuminatus* Chen & Xia (in Mu *et al.* 1979).

Re-examination of Hall's type material of both *Phyllograptus anna* and *P. ilicifolius* (discussed below) shows that both can be referred to *Phyllograptus*, *sensu stricto*.

From their illustrations, several of the forms described by Mu *et al.* (1979) are likely to represent true *Phyllograptus*. Their figures of '*P.*' *densus* (pl. 42, fig. 26, here synonymized with *typus*) and of *P. uniformis* (pl. 43, figs 17–19) both show what appears to be the central columella and a double row of fornical foramina and both have the characteristically pointed proximal end, as has their *P. acuminatus* (pl. 40, figs 10–13).

The correct generic reference for many described phyllograptoids, however, must remain in doubt until further details of their structure and development are known.

Phyllograptus typus J. Hall 1858

Figs 67a–f, 70a–h, 71a–l, 72–74; Pl. 4, figs 4, 10

- 1858 *Phyllograptus typus* J. Hall: 137.
 1865 *Phyllograptus typus* Hall; J. Hall: 119; pl. 15, figs 1–12.
 1947 *Phyllograptus ilicifolius* var. *major* Ruedemann: 318–319; pl. 53, fig. 21.
 1960 *Phyllograptus typus* Hall; Berry: 58; pl. 10, figs 13, ?1, ?11.
 1963 *Phyllograptus ilicifolius* var. *major* Ruedemann; Ross & Berry: 83; pl. 3, fig. 17.
 1976 *Phyllograptus densus* Törnquist; Legg: 27–28; pl. 8, fig. 39.
 1976 *Phyllograptus loringi* White; Braithwaite: 38–40; pl. 7, figs 29–31.
 1977 *Phyllograptus ilicifolius major* Ruedemann; Carter & Churkin: 14–15; pl. 1, fig. 4.
 1979 *Phyllograptus densus* Törnquist; Mu, Ge, Zhen, Ni & Lin: 123–124; pl. 42, figs 26, ?25.

Type material

LECTOTYPE. The specimen GSC 942c, figured by Hall (1865) as pl. 15, fig. 7, carries the label 'Type'. So far as we are aware, neither this specimen, nor any other, has been formally designated as type specimen. For the reasons discussed below (see 'Discussion') this specimen is not thought to be suitable for lectotype.

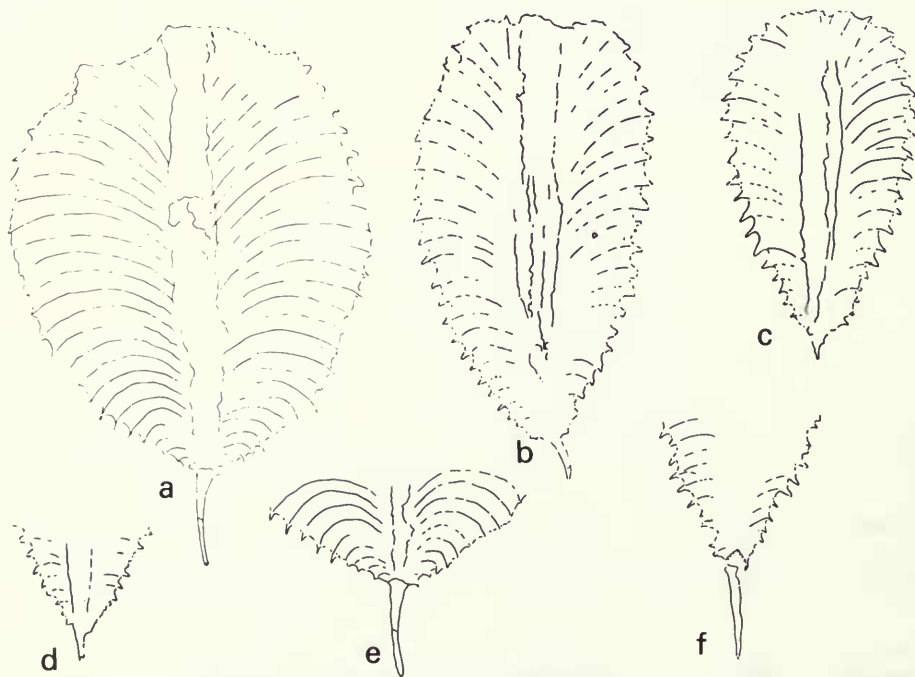


Fig. 67 *Phyllograptus typus* (Hall), type series. a, e, **lectotype**, GSC 942b, whole rhabdosome ($\times 2$) and proximal part ($\times 3$) respectively. Specimen figured by Hall (1865: pl. 15, fig. 1). b, specimen on same slab (GSC 942) as the original of Hall (1865: pl. 15, fig. 10), poorly preserved, and with small spine; $\times 3$. c, specimen on back of slab with original of Hall (1865: pl. 15, fig. 2); poorly preserved but outline and interthecal lines can be seen; $\times 3$. This specimen and that of b, with their pointed proximal regions and relatively inconspicuous spines, most closely match the Spitsbergen forms. d, proximal part of specimen in same slab as that of b; $\times 3$. f, proximal part of specimen preserved in same slab as b, showing pointed proximal region; $\times 3$.

Specimen GSC 942b (of the Geological Survey of Canada, Ottawa), figured by Hall (1865) as pl. 15, fig. 1 and refigured here (Fig. 67a) is here designated **lectotype**. It is about the best preserved of the specimens in the type series, none of which clearly shows details of the proximal end or of internal rhabdosome structure.

PARALECTOTYPES. Other specimens held by the Geological Survey of Canada and examined by us are GSC 942a, c–g, figured by Hall (1865) as pl. 15, figs 1, 2, 4, 5, 7, 10 and 12. In addition at least 10 other, unfigured specimens are present in the same slabs providing a relatively large population of type material. None are well preserved and many have lost much of the original carbonized periderm; it is possible that they have deteriorated considerably since Hall examined them. As far as can be determined, Hall's figures give a reasonably accurate portrayal of the specimens.

STRATIGRAPHIC HORIZON. Raymond (1914) lists *P. typus* from Zone B together with *Tetragraptus fruticosus* and Bulman (unpublished MS) adds *Didymograptus nitidus* and *P. ilicifolius*. The horizon is thus Bendigionian, or lower Arenig.

DESCRIPTION of type material. The sicula and details of the proximal region are not visible in any specimens, nor is internal rhabdosome structure. Rhabdosome outline varies widely from almost circular to elongate and the ratio of maximum width to length ranges from 0.29 to 0.85 with modal value of about 0.5 (Fig. 68). Most rhabdosomes have a prominent spine extending

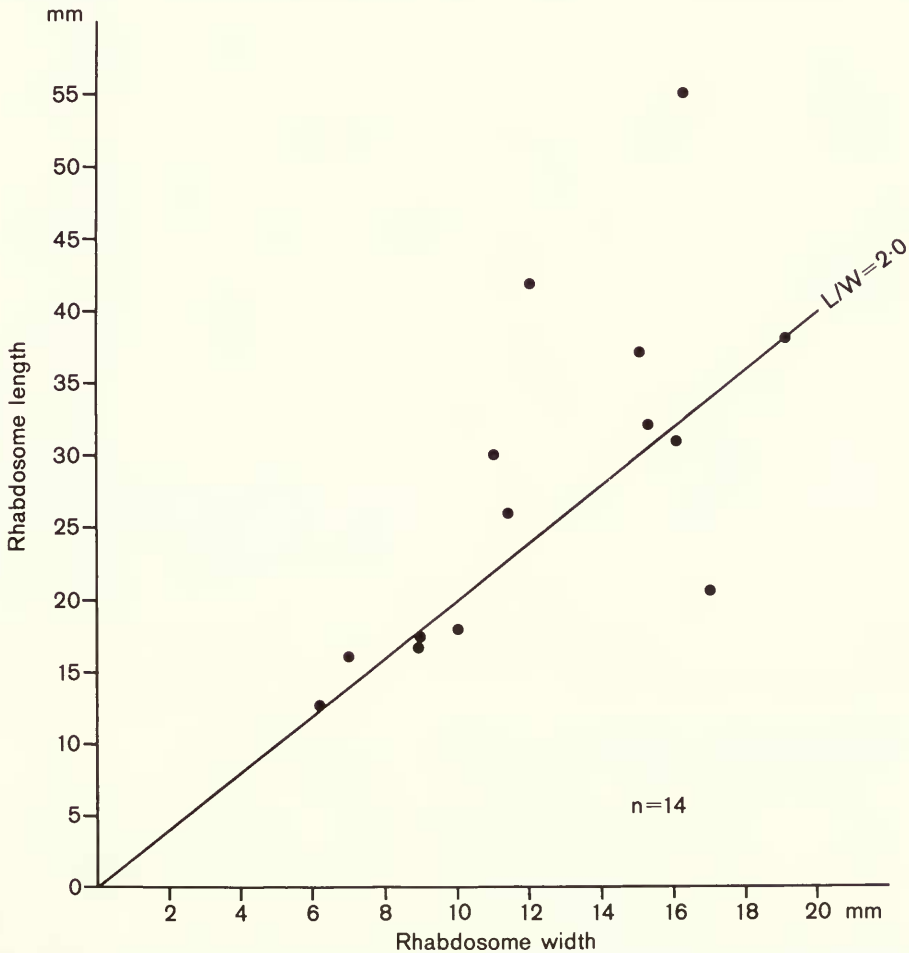


Fig. 68 *Phyllograptus typus* Hall, type population; rhabdosome width plotted against rhabdosome length.

from the proximal margin. Presumably this represents an enlarged virgellar spine. In the larger rhabdosomes the spine has a very broad base, and in a few it obscures the apertures of proximal thecae. In the specimens examined by us the length of the longest spine (that of Hall's pl. 15, fig. 7) is 6.5 mm, but the specimen of Hall's pl. 15, fig. 8 is shown by him to have a spine 10 mm long.

Thecae have relatively low initial inclination and are curved, strongly in the proximal region but progressively less strongly towards the distal end. Apertural outlines are not clearly shown in any specimen. Thecae are most densely spaced in the proximal region and most widely spaced in the distal parts of large rhabdosomes; the difference in thecal spacing between the two parts of the rhabdosome ranges from 1 to about 3 or 4 thecae in 10 mm. In large rhabdosomes measurements were taken in the mid-region of the rhabdosome for comparison with smaller forms. Spacing ranges from 10 to 13 in 10 mm, with a modal value of 10 (Fig. 69). The strong positive skew in the distribution may reflect the small sample size but may, in part, result from a weighting of the high (close spacing) end owing to inclusion of some small specimens.

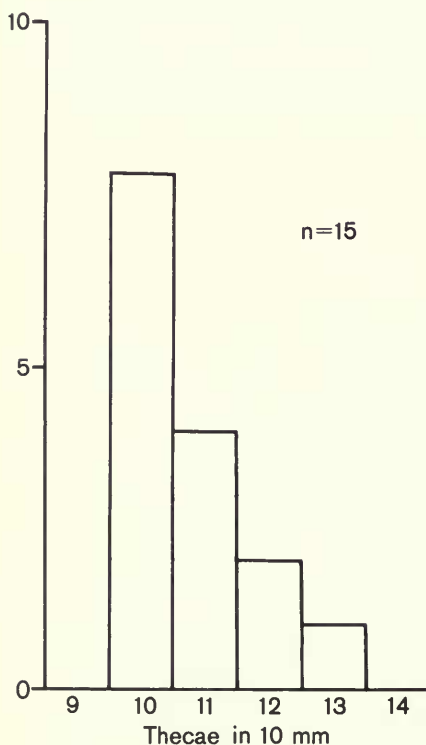


Fig. 69 *Phyllograptus typus* Hall, type population, frequency distribution of thecal spacing. The strong positive skew may simply reflect the small sample size but may, in part, result from attenuation of the high (close spacing) end of the range owing to the inclusion of some small specimens.

Range in rhabdosome form, spine development, thecal inclination and curvature is best appreciated by examining Hall's figures together with those figured here.

DISCUSSION. From Hall's figures it might be supposed that two populations are represented; those of his pl. 15, fig. 10 have relatively small rhabdosomes with less conspicuous sicular spines and more wedged-shaped proximal outlines whereas those of the remaining figures have large, rapidly expanding and sometimes irregularly shaped rhabdosomes and enormous sicular spines. None of the specimens of his fig. 10 are well preserved and the lectotype has been chosen from among the large specimens. The smaller wedge-shaped specimens are here regarded as conspecific with the Spitsbergen material assigned to *P. typus* and the question of their identity with the larger forms is crucial in view of the implications for the species of the

unusual (and diagnostic) development and internal structure revealed in the Spitsbergen material. Fortunately, among the unfigured specimens in Hall's collection is a group (particularly those on the slab, 942d, with the specimen of pl. 15, fig. 2) which bridges the gap and indicates that all of Hall's material most probably represents a single population, with wide variability in rhabdosome size and outline and in development of the sicular spine. There are no other taxa present and the lithology of all slabs is the same, a dark carbonate-rich siltstone.

The large forms may simply be 'overgrown' or 'gerontic' rhabdosomes. Continued growth of proximal thecae would increase the rate of rhabdosome expansion and result in a more rounded proximal end. Proximal thecal curvature would increase and their distal portions would become more markedly pendent. These features are well shown by the lectotype. The slightly irregular outlines of several rhabdosomes suggest variation in growth rate and the massive sicular spine indicates overgrowth, presumably by additional layers of cortical tissue. The process seems to be most developed in the specimen (GSC 942c) of Hall's pl. 15, fig. 7 and for this reason the specimen is deemed unsuitable for lectotype.

Phyllograptus ilicifolius major Ruedemann (1947) is clearly a synonym of *P. typus*. The holotype (Ruedemann 1947: pl. 53, fig. 21, refigured by Ross & Berry 1963: pl. 3, fig. 17) from Nevada has a proximal spine, proximally pointed rhabdosome and similar thecal spacing. Its distinction from *P. typus* was discussed neither by Ruedemann nor Ross & Berry. The specimen figured by Carter & Churkin (1977: pl. 1, fig. 4) as *P. ilicifolius major* has a larger rhabdosome and more prominent proximal spine, like that of the Levis forms, but slightly more closely spaced thecae (12–14 in 10 mm). The horizon for the species in western U.S.A. is given as *D. protobifidus* Zone. The specimen figured by Legg (1976: pl. 8, fig. 39) from Fauna 3b (Bendigonian–Chewtonian), as *P. densus* Törnquist, bears a proximal spine and pointed proximal end; its higher thecal count (13–14 in 10 mm) may reflect its relatively small size and be equivalent to the more densely spaced proximal thecae of large specimens. Specimens figured as *P. densus* from Zone N3b of *Didymograptus deflexus* (about Chewtonian) of south-west China by Mu *et al.* (1979: 123–124; pl. 42, figs 24?, 25?, 26) show an axial structure with what appears to be a central columella separating a double row of fornicial foramina. Overall rhabdosome shape, thecal inclination and curvature lie within the range of *P. typus*, with which it is included here. Braithwaite's description and figures (1976: 38–40; pl. 7, figs 29–31) of supposed *P. loringi* White, from his Zone 5 of Utah, match well with *P. typus*.

The wide range in rhabdosome size and proportions was discussed and illustrated by Hall, and also commented upon by Ruedemann (1947) and Berry (1960). These characters thus appear to be of limited use in diagnosis. However, the narrow, elongated rhabdosome form of *Pseudophyllograptus angustifolius* is rarely achieved in the various North American and Spitsbergen populations in which a broad oval outline is most common. Similarly, thecal spacing, although strongly modal at 10 thecae in 10 mm, ranges widely and is unlikely to justify the faith placed in it as a diagnostic character by some authors. Because of the denser thecal spacing in immature rhabdosomes it is likely that they have often been confused with *Phyllograptus anna* Hall (see p. 286).

Spitsbergen material

STRATIGRAPHIC HORIZON. Specimens with the diagnostic axial structure are known from 40–43 m, 75 m and 88–90 m levels in units V_1 – V_2 of the Valhallfonna Formation. Specimens showing the proximal spine are present at the 25 m and 75 m levels. All phyllograptoids of this interval (25 m–90 m) appear to comprise a single variable group and are included in the species. In addition, specimens from the 12–15 m and 93 m levels have a pointed proximal margin, a similar range in rhabdosome shape, and are also included. Total range is thus 12 m–93 m level, V_1 – V_2 , and embracing all the middle Arenig.

MATERIAL. F3716, F3801, F4005, F4055, F4084, F4098, F4169, F4270, F4271, ?F4218. PMO NF625, NF636, NF751, NF760, NF765, NF2046, NF2049, NF2050, NF2065, NF2815, NF3173, NF3390–1. SM A105794, A105810, A109732, A109737.

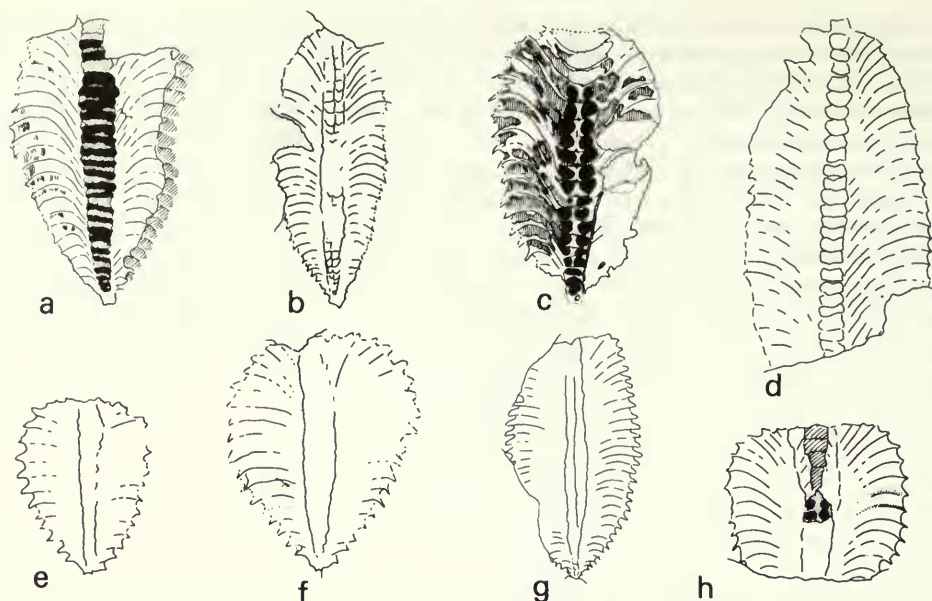
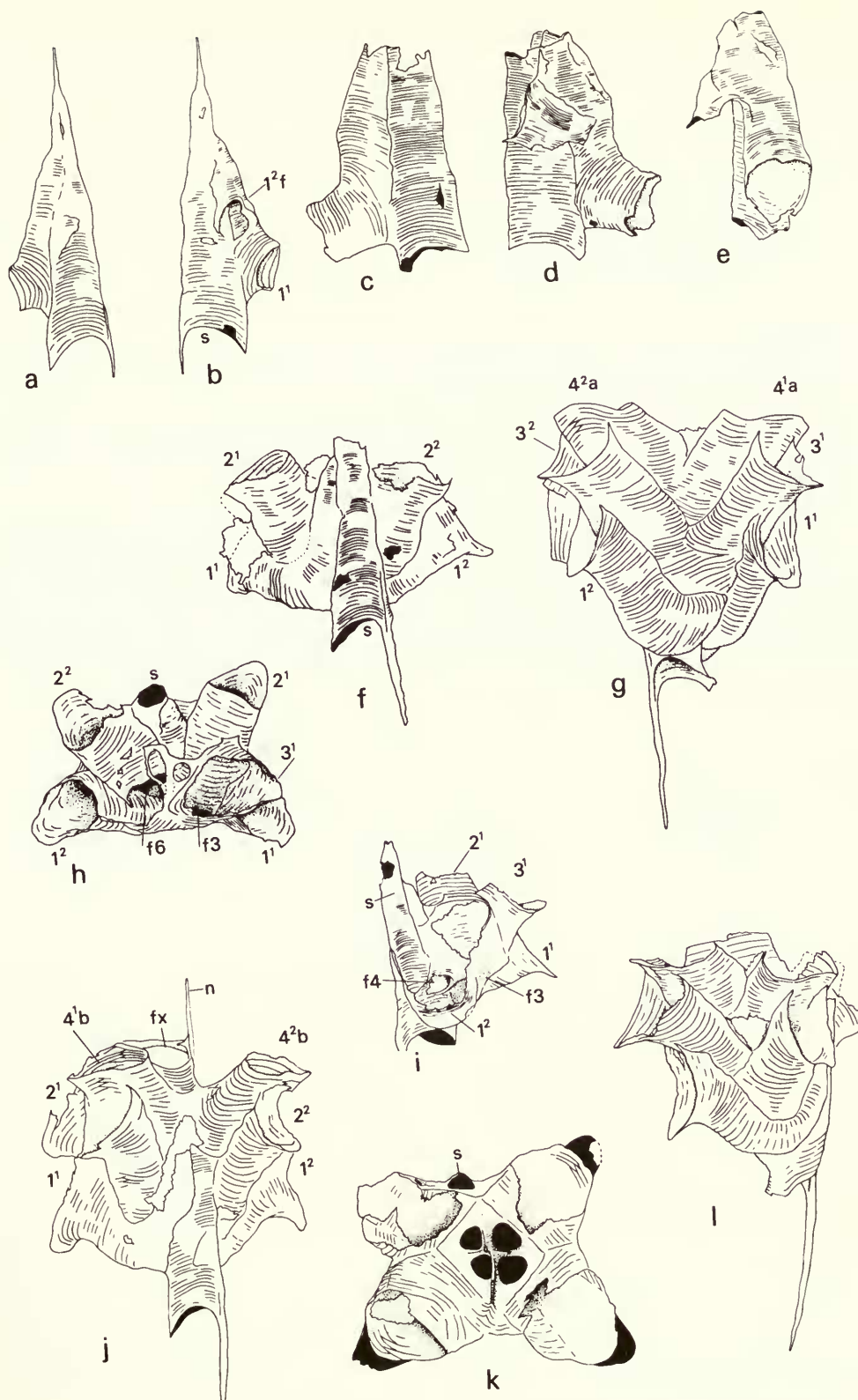


Fig. 70 *Phyllograptus typus* Hall, Spitsbergen population. a, PMO NF760, specimen in relief in limestone showing transverse cross sections of upper thecal series, broken off near the axial region and exposing short lengths of interthecal septa (stippled). 74.5 m above base of Olenidsletta Member, type section; $\times 4$. b, NF3362, rather poorly preserved specimen from 40–43 m above base of Olenidsletta Member; $\times 2$. c, NF3173, specimen in relief and partially etched revealing double row of internal foramina and central columella. Same horizon as a; $\times 4$. d, SM A109737, proximal end broken off. 93 m above base of Olenidsletta Member, type section; $\times 2$. e–g, PMO NF3176, NF2049 and NF2065 respectively. Virgella clearly showing in f. All from 23–25 m above base of Olenidsletta Member, southern section; e and f $\times 2$; g $\times 3$. h, SM A109732, upper stipe broken off to reveal, near mid length, the foramina; $\times 3$. This form resembles *P. rotundatus* Mønsen: see Pl. 4, fig. 7.

DESCRIPTION OF ISOLATED MATERIAL. Sicula bears a short nema up to 0.5 mm long. Details of the prosicula are unknown. The metasicula bears a prominent virgella which projects beyond the apertural margin by up to 0.8 mm. It appears to be most robust in the more advanced growth stages, suggesting that it was built up with cortical tissue after completion of growth of the

Fig. 71 *Phyllograptus typus* Hall, isolated growth stages. a, b, PMO NF751, early growth stage with theca 1¹ partly formed and the foramen (1^{3f}) to th1² formed, obverse and reverse views. Note weakly developed virgella and antivirgellar side origin of th1¹. c, d, e, NF3390, incomplete growth stage obverse, reverse and lateral (stipe¹ side) views respectively. Theca 1¹ has diverged from the sicula and the arch through which th2¹ would grow can be seen. f, h, NF3391, growth stage with apex of sicula broken off; first 4 thecae (1¹, 1², 2¹, 2²) have formed. Obverse view (f) shows sicula has not yet become enveloped by proximal thecae, and prominent virgellar spine. Top view (h) shows the commencement of formation of columella, and first interthecal foramen (from th3¹ to th4^{1a}) and the foramina, f3 (2¹/3¹) and f6 (2²/4^{2a}). s = sicula. i, NF622, specimen dissected to reveal foramen (f4) between th1² and th2². Position of foramen (f3) between th2¹ and th3¹ indicated. Thecae 2², 3² and part of 1² have been removed. j, NF3312, advanced growth stage with three thecae on each stipe showing reclined attitude of distal portions of proximal thecae. Note that apical part of sicula has become enveloped by thecae 4^{1b} and 4^{2b}. Fornix (fx) lies behind, and is *not* attached to, nema (n). g, k, l, NF3314, viewed from interangle between stipes ^{1a} and ^{2a} (g), ^{1a} and ^{1b} (l) and top (k). Top view shows four quadrant-shaped interthecal foramina in square plate-like structure formed of the four adjacent interthecal septa in the axial region. Note that thecae of adjacent thecal series remain in lateral contact for some distance beyond the central axial region. All specimens from 74.7 m above base of Olenidsletta Member, type section. All $\times 30$.



sicula and the first few thecae. The downward deflection of fuselli into the virgella can be traced back to the mid-region of the metasicula, suggesting that the virgella begins to form, and the ventral side of the sicula is defined, at an early stage. The dorsal margin of the sicula is extended into a prominent lip which projects well beyond the level of the base of the virgella. This feature, also, develops at an early stage of growth of the metasicula.

Length of the sicula, to the tip of the dorsal margin, is 1.2–1.4 mm, and dorsoventral width at the aperture ranges from 0.3 to 0.35 mm. Variability in the length of that portion of the metasicula which projects below the ventral walls of the first two thecae is shown in Fig. 71f, j.

The sicula remains free on the obverse side of the rhabdosome up to the level of $th2^1$, after which its apical portion becomes incorporated within the rhabdosome wall (Fig. 71j). The nema becomes embedded along the junction of the two thecal series, 1^b and 2^b . The nema is not continuous with the axial column but is linked with it by fornice ('flying buttress' structures) described below.

The distal portions of all proximal thecae are directed upwards at about 45° to the stipe axis, and the proximal rhabdosome margin has a rather pointed outline.

PROXIMAL DEVELOPMENT. This has been determined from two early growth stages (Fig. 71a–e) and several advanced growth stages, the outer rhabdosome walls of some of which have broken away exposing internal structure.

Details of the prosicula are unknown. Origin of $th1^1$ is not clear but it appears to arise from either the prosicula or from near the top of the metasicula, on the dorsal side.

In its early development it forms a 'hood' which soon expands out into an arch allowing room for the developing $th2^1$ (Fig. 71e). Theca 1^1 grows well down the sicula before curving sharply away and looping around the base of $th2^1$, its distal portion growing strongly upwards and outwards and forming the basal theca of stipe 1^a . The dicalycal theca, 1^2 , originates *via* a broad foramen from $th1^1$ (Fig. 71b), grows down and across the sicula in a dextral sense and curves

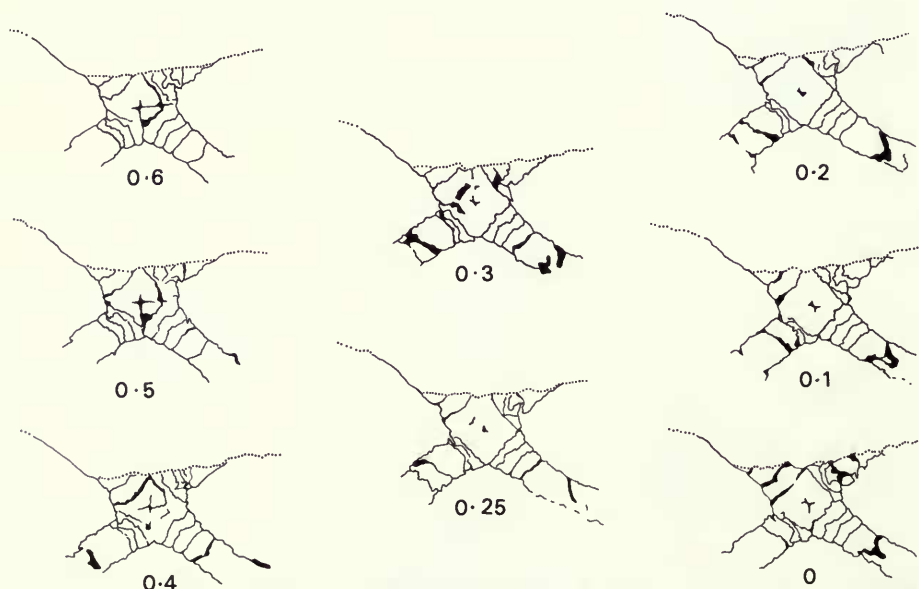


Fig. 72 *Phyllograptus typus* Hall, serially ground sections, PMO NF765, $\times 4$. Specimen has partially collapsed but is sufficiently intact to reveal some details of internal structure. Section level shown by number in mm above basal section. Sections 0–0.25 show cruciform columella in centre of axial region with wide openings (fornical foramina) between thecae of laterally adjacent series. Sections 0.4–0.6 pass through the region of the fornice, section 0.6 intersecting two fornice. Because of the slight spiral offsetting of fornice (and possibly damage suffered by the specimen) no single section passes through all four fornice.

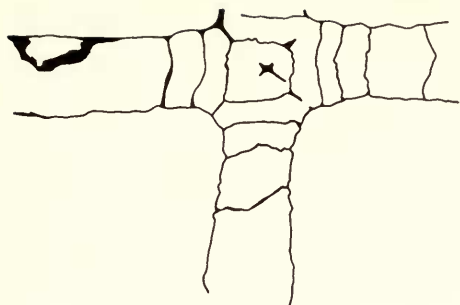


Fig. 73 *Phyllograptus typus* Hall. PMO NF760, transverse section through mature part of rhabdosome to show internal structure. Top stipe lies off edge of slab. Cruciform columella in centre with wide openings (fornical foramina) between thecae of laterally adjacent thecal series, except for where fornix has been intersected (lower right); $\times 8$.

sharply away from it at about the same level as does $th1^1$. It then loops around the base of the developing $th2^2$ and grows upwards and outwards forming the basal theca of stipe 2a and matching, in its distal region, the attitude of the distal part of $th1^1$. The first two thecae are thus considerably longer than subsequent proximal thecae. Theca 2^1 arises shortly after the origin of $th1^2$ and grows across the line of $th1^1$, in its upward growth forming the basal theca of stipe 1b . It gives rise to the dicalycal theca, 3^1 , through a small round (? resorption) foramen ($f3$, Fig. 71h, i). Theca 4^1b is given off through a wide foramen as is the 'sibling' theca 4^1a . At this stage of development, stipe 1a is comprised of three thecae, 1^1 , 3^1 and 4^1a and stipe 1b is comprised of two thecae, 2^1 and 4^1b .

On the $th1^2$ side, $th2^2$ arises through a small round foramen ($f4$) like that of $th3^1$ and forms the basal theca of stipe 2b . It gives off, through a wide open foramen ($f6$, Fig. 71h), the dicalycal $th3^2$ which in turn gives off, firstly $th4^2b$ then $th4^2a$. At this point, stipe 2a is composed of the three thecae, 1^2 , 3^2 and 4^2b and stipe 2b is composed of the two thecae, 2^2 and 4^2b . The four stipes are developed, from this point on, by unicalycal budding.

INTERNAL RHABDOSOME STRUCTURE. Internal structure of the mature rhabdosome has been determined from a partially etched specimen (Fig. 70c) in which one thecal series has broken away exposing the axial region, from serially ground sections (Figs 72, 73) of the mature part of the rhabdosome, and from advanced growth stages (Fig. 71i-l).

The four stipes are united along their dorsal margins, not by a set of four median septa as in *Pseudophyllograptus angustifolius* (clearly illustrated by Holm 1895: pl. 14, fig. 12) but by a complex internal network of struts and horizontal perforated plates. The interthecal septum between thecae in any thecal series (i.e. in any one 'stipe') becomes sharply horizontal as the axial region is approached and is perforated by a comparatively small quadrant-shaped aperture, the interthecal foramen (Fig. 71k). The septum is united with its neighbours of the

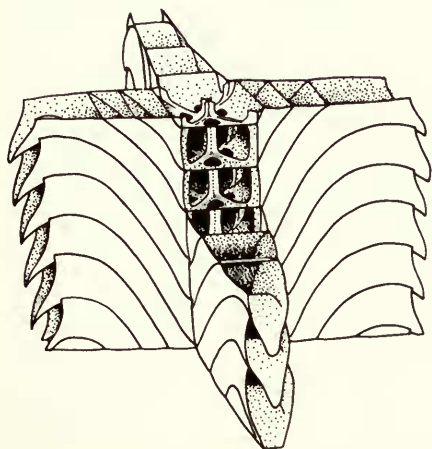


Fig. 74 *Phyllograptus typus* Hall. Cut-away diagram showing internal rhabdosome structure.

adjacent thecal series in the axial region to form an axial platform. Each segment of the platform is slightly offset from the level of the adjacent segment and the platform is spirally curved. Thus in the section series (Fig. 72) the four interthecal foramina are not intersected by any one section. The lateral thecal wall within the axial region is largely reduced to an arched strut, like a flying buttress, here termed the *fornix*, one at the level of each interthecal septum. A wide opening, the *fornical foramen* is thus left between thecae of adjacent thecal series.

The innermost margins of the lateral thecal walls are united to form a thickened column, the *columella*, at the centre of symmetry of the rhabdosome, clearly seen in serial sections (Fig. 72). Fig. 71k shows that the columella develops independently of the sicula and nema.

Growth stages indicated that the fornices are primary structures formed during the building of the rhabdosome and the fornical foramina are not secondary resorption features, like the accessory foramina in *Pseudotrigraptus minor* (Fortey 1971).

COMMENTS ON PROXIMAL DEVELOPMENT AND STRUCTURE. Origin and subsequent growth of theca 1¹ on the antivirgellar side of the sicula is a departure from the usual dichograptoid pattern. The thecal budding plan is shown in Fig. 75. Initial development conforms with the isograptid type and is dextral.

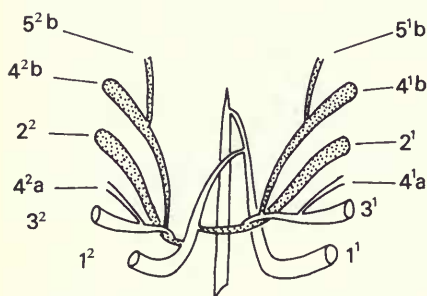


Fig. 75 *Phyllograptus typus* Hall. Thecal diagram for proximal development.

The second-order dichotomy on the stipe¹ side is based on dicalycal th3¹ and is sinistral, whereas that on the stipe² side is based in th3² and is dextral. All three dicalycal thecae thus grow out on the reverse side of the rhabdosome. The interthecal foramina which open into thecae 1², 3², 4^{1a}, 4^{1b}, 4^{2a} and 4^{2b} are large, open, primary apertures, but those opening into thecae 2² and 3¹ are small and round and are possibly resorption foramina. That opening into th2¹ has not been clearly seen but appears to be large and primary.

A striking feature of the proximal region is the reclined attitude achieved by the proximal thecae, particularly thecae 1¹ and 1², shown clearly by the isolated growth stages (Figs 71g, j). In this respect, the species (and the genus) is unique among dichograptoids, even among such scandent forms as *Skiagraptus*, *Cardiograptus* and *Pseudophyllograptus* where proximal thecae grow essentially downwards or outwards rather than upwards. It resembles, rather, the early diplograptids especially streptoblastic glyptograptids of the *austrodentatus* group (Bulman 1963).

Another unusual feature is that the first two thecae 1¹ and 1² form the basal thecae of the adjacent pair of second-order stipes, ^{1a} and ^{2a} respectively. This is an unexpected departure from the general graptolite rule of maintaining symmetry in development and an important point of difference from *Pseudophyllograptus* where the initial thecae do not form part of the second-order stipes but lie below, and medially between them, as in *Tetragraptus bigsbyi*.

DESCRIPTION OF NON-ISOLATED MATERIAL. Rhabdosome size and shape are extremely variable and scarcely any two specimens, even from the one bedding plane, are closely similar. Maximum rhabdosome length is 35 mm, maximum width is 14 mm. The ratio of maximum width to length ranges from 0.3 to 0.65 (Fig. 76) and outline shape varies from squat and ovate to elongate. The distal margin of incompletely grown rhabdosomes is bluntly terminated (Fig. 70e, h). The proximal margin tapers to a point and the sicular (virgellar) spine is only rarely

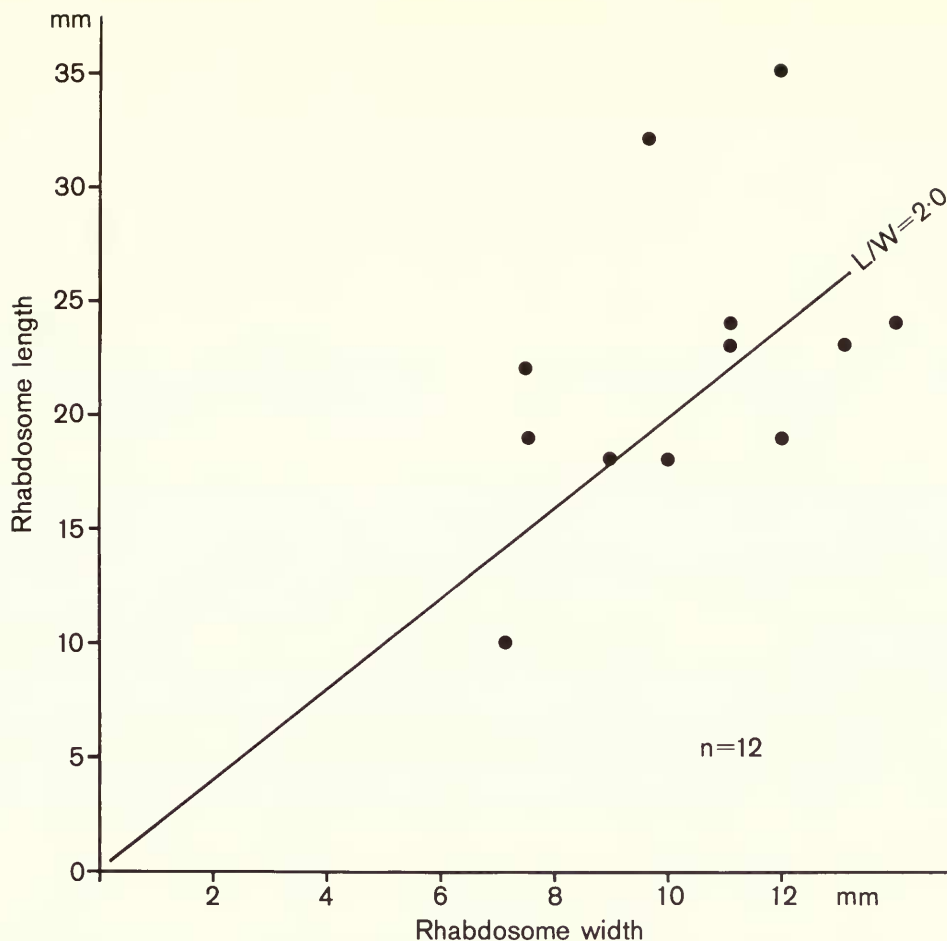


Fig. 76 *Phyllograptus typus* Hall, Spitsbergen population. Rhabdosome maximum width plotted against rhabdosome length, showing wide variation in rhabdosome proportions. Incomplete specimens (not plotted) show that total range of variation is greater than that shown.

visible. The attitude of proximal thecae is seldom determinable in flattened material but specimens from the 25 m level (Fig. 70e, f) appear to have initial thecae that are somewhat less reclined than those from the 75 m level. However, isolated but flattened growth stages from the 15–23 m level (A105810) show strongly reclined early thecae.

In their initial growth, thecae have relatively low inclination (40° or less) but curve sharply and reach an inclination greater than 90° near their apertures. Their lateral width is greatest near the axial region where they have a transversely tabular cross section (Fig. 70a). Except for the proximal few thecae, which have free ventral walls, thecae overlap for almost their entire length. Apertural margins are projected into a prominent ventral lip. The axial region of the rhabdosome increases in width from about 0.5 mm near the proximal end to over 2 mm in the middle part of the rhabdosome (Fig. 70c).

Thecae are spaced 10 to 14 (most commonly 12) in 10 mm in the mature part of the rhabdosome (Fig. 77). Thecal spacing is denser in the proximal region and immature rhabdosomes give thecal counts of 16 or more in 10 mm. There is no progressive change in thecal spacing in successively higher stratigraphical levels (Fig. 78).

FUNCTIONAL INTERPRETATION. The functional purpose of the large fornicular foramina and struts, in place of a continuous peridermal wall, between thecal series in the axial region can only be

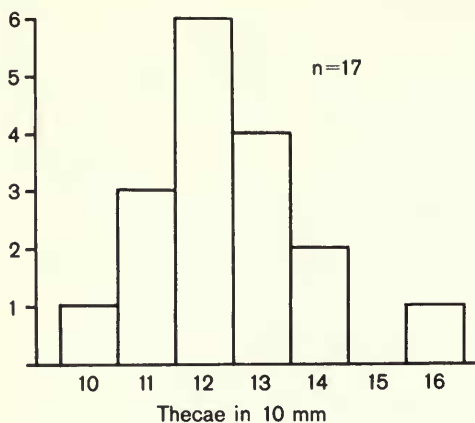


Fig. 77 *Phyllograptus typus* Hall. Frequency distribution of thecal spacing (taken to nearest whole number) in Spitsbergen population, showing wide range of variation.

guessed at. They would have had the effect of lightening the rhabdosome without reducing its rigidity, and thereby aiding in buoyancy. This is unlikely to have been their primary function, however, since it will be seen from the sections that the amount of weight saved is a minimal proportion of the total rhabdosome weight. It seems more likely that they existed to allow communication, either direct or indirect, between zooids of adjacent thecal series, but for what purpose is unclear.

What is clear is that construction of the axial skeletal structures required highly integrated activity on the part of the graptozooids, throughout the development of the rhabdosome, and closely concordant budding within each of the four thecal series. The columella appears to be without analogy among the graptoloids unless it is equivalent to the pseudovirgula of monograptids. It is built up along with the rhabdosome and never projects far beyond the distal

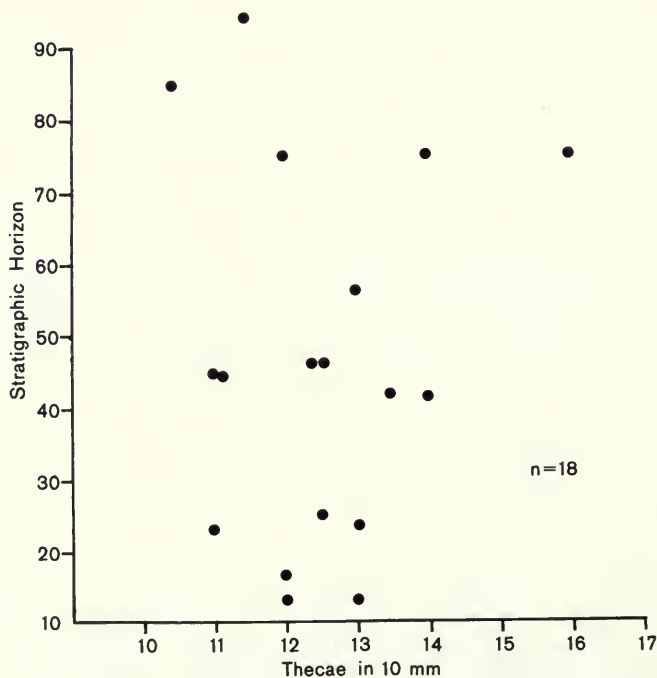


Fig. 78 *Phyllograptus typus* Hall. Thecal spacing (taken to nearest whole number) in Spitsbergen specimens plotted against stratigraphical level (metres above base of Olenidsletta Member). There is no progressive trend through the considerable stratigraphic interval of its occurrence.

rhabdosome margin. It could thus not have acted as an attachment organ and there is no evidence that the rhabdosome was suspended, although the sicula, with its short nema, and earliest growth stages may have been.

DISCUSSION. The species is readily distinguished by its peculiar internal rhabdosome structure and proximal development and structure. Unfortunately neither of these regions is readily examined in flattened specimens. In incompletely flattened specimens where the upper stipe has broken away right back to the axis, the fornicular foramina and columella can be seen (Fig. 70c); where the inner margin of the upper stipe still remains, as in Fig. 70a, d, only the matrix-filled thecal interiors are exposed, providing no clue as to internal structure.

The pointed proximal end can usually be determined in flattened specimens, but angle of inclination of proximal thecae is commonly obscure.

The Spitsbergen form most closely matches *Phyllograptus typus* Hall and *P. ilicifolius* Hall. The absence of an overgrown virgellar spine from mature rhabdosomes suggests *P. ilicifolius*, but the persistently pointed proximal rhabdosome outline and wide variability in rhabdosome form and proportions, together with the large size attained by some rhabdosomes and the prominence of the virgellar spine in growth stages, suggest that the Spitsbergen form is best identified with *Phyllograptus typus*. The slightly higher thecal spacing modal value may be a reflection of the generally smaller size of rhabdosome in the Spitsbergen populations, and thus of the closer thecal spacing in the proximal region, but the wide range is similar in both the Spitsbergen and Levis populations.

Internal rhabdosome structure and proximal development and structure are, of course, unknown in the type population of *typus* and these features, revealed by the Spitsbergen material, provide important diagnostic characters for the species and for the genus *Phyllograptus*.

RELATIONSHIPS AND ANCESTRY. Several features of development and structure indicate that the species is unlikely to have been derived from an ancestor of *Tetragraptus bigsbyi* type, as seems probable for *Pseudophyllograptus* (Bulman 1936a). The rhabdosome could not have been formed by, in effect, concrescence of the stipes of a reclined tetragnostid. While it could be argued that the internal rhabdosome structure was secondarily derived from a 'normal' pseudophyllograptid, the strongly reclined initial thecae and their alignment with the two adjacent stipes 'a and 'a, the presence of a virgellar spine, and the antivirgellar development of th1' are all features unknown in any tetragnostid.

It is here thought that sicular morphology and the antivirgellar origin and growth of th1' may provide a clue to its relationship with other species. These features would unite it with such species as *Xiphograptus formosus formosus* and *X. formosus svalbardensis*. Ancestry of such a group, however, remains unclear.

Phyllograptus anna Hall 1865

Fig. 79a–d

1865 *Phyllograptus anna* J. Hall: 124; pl. 16, figs 11–16.

1902 *Phyllograptus anna* Hall; Elles & Wood: 101–102, figs 60a–b; pl. 13, figs 6a–f.

1904 *Phyllograptus anna* Hall; Ruedemann: 714–717, text-figs 98–99; pl. 15, figs 23–30.

1979 *Phyllograptus anna* Hall; Cooper: 68, fig. 40; pl. 6g; pl. 10g.

LECTOTYPE. Slab GSC 938a, figured by Hall (1865: pl. 16, fig. 15) and refigured here (Fig. 79a) is here designated as **lectotype**. Preserved in the Geological Survey of Canada Museum, Ottawa.

PARALECTOTYPES. GSC 922f, 938 and 938a; specimens figured by Hall (1865: pl. 16, figs 11, 13, 14, 15, 16) held by the Geological Survey of Canada. The slab 938a has, in addition, more than 60 other rhabdosomes of the species, of which three are figured here (Fig. 79b–d).

STRATIGRAPHIC HORIZON. Raymond (1914) and Bulman (unpubl. MS) list *P. anna* from Zone C3 of the Levis Shales at Levis, Quebec, together with *Didymograptus bifidus*.

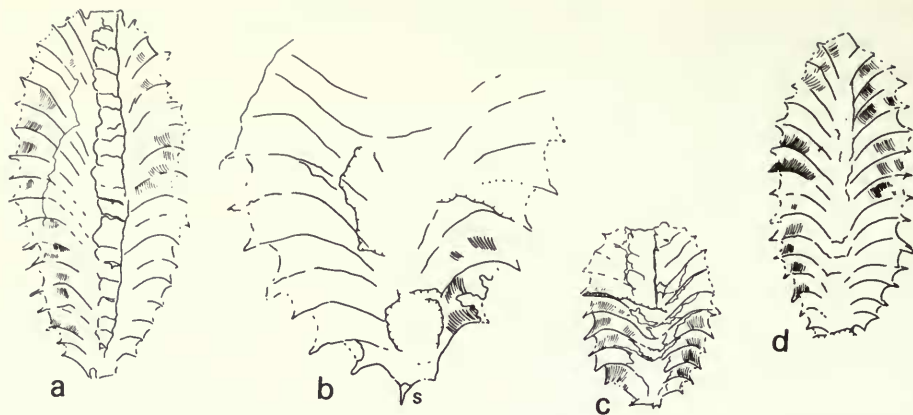


Fig. 79 *Phyllograptus anna* Hall, type series. a, **lectotype** GSC 938a, original of Hall (1865: pl. 16, fig. 15); $\times 4$. b, proximal region of specimen in same slab as lectotype showing incipient spine on sicle (s) and reclined growth of proximal thecae; $\times 8$. c, small specimen in same slab as lectotype clearly showing proximal thecae; $\times 4$. d, specimen in same slab as lectotype; $\times 4$.

DISCUSSION. The species is included in the present discussion in order to clarify its relationship with *Phyllograptus typus* and *Pseudophyllograptus angustifolius*. Traditionally it has been recognized primarily by its small size and closely-spaced thecae. From the refigured lectotype and paratypes, however, it can be seen that several features of rhabdosome morphology are shared with *P. typus*. The low initial angle of thecal inclination and the reclined attitude of the proximal thecae are particularly noticeable. Furthermore, in the specimens of Fig. 79b, c the sicle protrudes from the proximal end of the rhabdosome and bears a short virgellar spine. The general aspect of the proximal region is undoubtedly similar to that of *P. typus* and *P. ilicifolius*, with which species it is here thought to be most closely related. It is therefore included in the genus *Phyllograptus*, *sensu stricto*.

Thecal spacing is difficult to determine because of the small size of the rhabdosome, but is approximately 6.5 in 5 mm (i.e. 13 in 10 mm) measured in the middle third of the rhabdosome of the two largest figured rhabdosomes. This figure is slightly smaller than that given by Hall (14.5 in 10 mm) and Elles & Wood (14–16 in 10 mm), and considerably smaller than that given by Ruedemann (16–20 in 10 mm). Ruedemann's illustrations, however, would suggest that at least some of his specimens have a somewhat wider spacing of about 14–16 in 10 mm when measured as above. Internal rhabdosome structure cannot be clearly determined in any of the type specimens.

The species closely resembles early growth stages from Spitsbergen assigned to *P. typus* and it is possible that it represents a growth stage of *typus* or *ilicifolius*. Unfortunately there are no early growth stages of either *typus* or *ilicifolius* from Levis available for comparison. From the Spitsbergen growth stages it is distinguished by its tapered, rather thin, bluntly terminated distal end, suggesting that it represents a mature rhabdosome rather than a growth stage. On this rather tenuous evidence, and until stratigraphically controlled population studies are carried out on the Levis section, *Phyllograptus anna* is maintained as a distinct species.

The forms described as *P. anna* by Braithwaite (1976: 32–35; pl. 7, figs 9–21) have truncated distal rhabdosome margins, suggesting that they are immature rhabdosomes of a larger form such as *P. typus* or *P. ilicifolius*. However, the apparent lack of a virgella, even in early growth stages, casts doubt on their identity with Hall's species.

Phyllograptus ilicifolius Hall 1858

Fig. 80a, b

1858 *Phyllograptus ilicifolius* J. Hall: 139.

1865 *Phyllograptus ilicifolius* Hall; Hall: 121–123; pl. 16, figs 1–9.

LECTOTYPE. GSC 940, figured by Hall (1865: pl. 16, fig. 4) and refigured here (Fig. 80a), is here designated as **lectotype**. It is held by the Geological Survey of Canada.

PARATYPES. GSC 940a–d, specimens figured by Hall (1865: pl. 16, figs 1–3, 5–9), and more than 20 other mature rhabdosomes in the same slabs, of which one is figured here, Fig. 80b. All held by the Geological Survey of Canada.

STRATIGRAPHIC HORIZON. Raymond (1914) and Bulman (unpublished MS) list the species from Zones A and C1–3, and Bulman further records it in Zone B, with *Phyllograptus typus*.

DISCUSSION. The new information from the Spitsbergen phyllograptoids has made it necessary to re-examine the type series of *P. ilicifolius*. From material here figured it is apparent that the species bears close resemblance to *Phyllograptus typus*. Most significant is the fact that a true *Phyllograptus* rhabdosome structure can be determined from the type specimens, which are preserved in slight relief. One incomplete specimen lies on the edge of the slab containing the specimen of Hall's (1865) pl. 16, fig. 9. The edge of the slab was ground back to reveal a cross section of the rhabdosome, and the isolated central cruciform columella was clearly seen. Several other specimens, such as that figured in Fig. 80b, are preserved so as to expose the double row of fornal foramina. The evidence thus conflicts with Hall's own (1865: pl. 16, fig. 10) interpretation of rhabdosome structure which appears to be based on *Pseudophyllograptus* rather than *Phyllograptus*, *sensu stricto*.

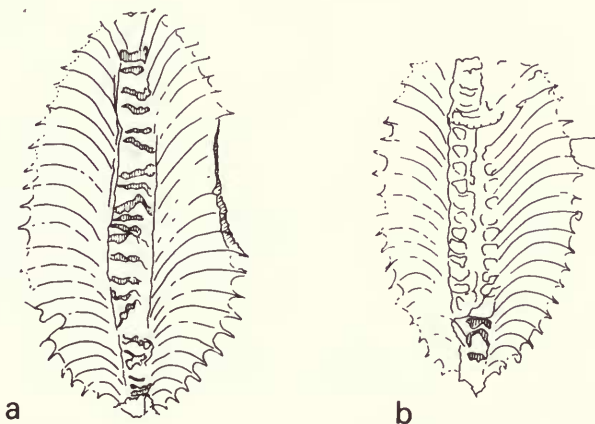


Fig. 80 *Phyllograptus ilicifolius* Hall, type series. a, **lectotype** GSC 940, original of Hall (1865: pl. 16, fig. 14). b, GSC 940c, specimen on slab with that figured by Hall (1865: pl. 16, fig. 9), showing double row of fornal foramina. Both $\times 3$.

In a few specimens (Fig. 80b) the proximal end is well enough exposed to reveal a blunt sicular spine and the reclined attitude of the initial thecae is clearly seen in many specimens. There is no doubt that the species is a true *Phyllograptus*.

Thecae have a low initial angle of inclination, as in *typus*, and are strongly curved in the proximal region. Thecal spacing (12–16 in 10 mm, Fig. 81) is slightly closer than in Hall's *typus* but shows a similar, wide, range. The chief distinctions from Hall's *typus* are the lack of a prominent sicular spine (even in similar-sized rhabdosomes), a less tapered proximal rhabdosome outline and an apparently smaller maximum rhabdosome size. It may be argued that these are insufficient to maintain it as a distinct species, but it seems best to retain *P. ilicifolius* until population studies can clarify its distinctness or otherwise from *P. typus* at Levis. There is no doubt that the two forms are closely related. It is clear, from examination of the literature, that there has been much confusion in distinguishing between the two species, and a careful examination of specimens is needed before synonymy can be attempted.

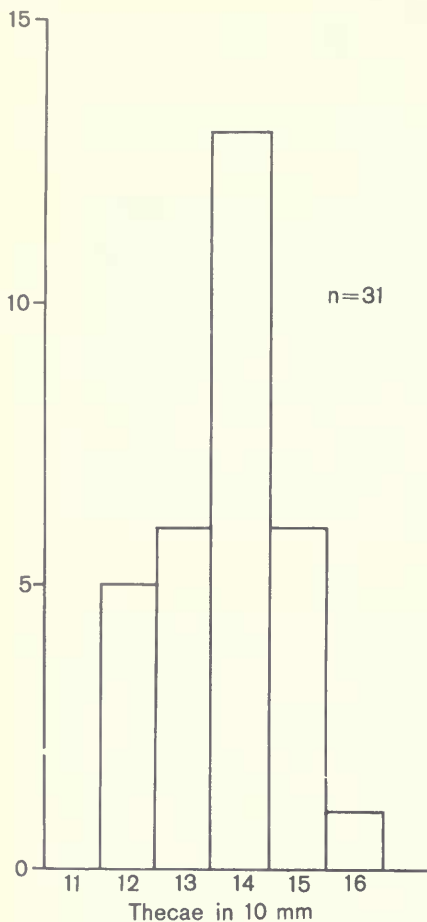


Fig. 81 *Phyllograptus ilicifolius* Hall, type series. Frequency distribution of thecal spacing (taken to nearest whole number).

Phyllograptus ? sp. nov.

Fig. 82

STRATIGRAPHIC RANGE. 17–25 m level, Olendisletta Member, V₁b.

MATERIAL. PMO NF2047, NF3183.

DESCRIPTION AND DISCUSSION. Although represented only by poorly preserved or incomplete material, the species is distinguished by the extremely close spacing of its thecae. Distally, thecal spacing is wider and measures about 4 in 2.5 m (equivalent to 16 in 10 mm). All rhabdosomes are very small (less than 12 mm long) and can be compared only with the proximal portions of other species such as *Phyllograptus anna*, from which they can be seen to differ in the closer spacing of their thecae.

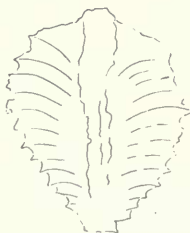


Fig. 82 *Phyllograptus*? sp. nov. PMO NF2047; small rhabdosome with closely spaced thecae. 25 m above base of Olendisletta Member, southern section; $\times 4$.

Although there appears to be no available name for the species, the poor preservation of our material precludes formalizing it as a new species. It may well be represented elsewhere in the world by those specimens, currently attributed to *Phyllograptus anna*, with a thecal count of 16–20 (e.g. Ruedemann 1947: 316 or *P. elegans* Ge (in Mu *et al.* 1979)). Internal rhabdosome structure is uncertain but from NF3183, in relief, appears likely to be that of *Phyllograptus* rather than *Pseudophyllograptus*.

Genus *XIPHOGRAPTUS* nov.

TYPE SPECIES. *Didymograptus formosus* Bulman 1936a.

DIAGNOSIS. Phyllograptines having extensiform or declined didymograptid rhabdosome habit. Small growth stages show long, slender virgellar spine, and antivirgellar origin of th1¹. Sicula short, about 1.5 mm or less. Proximal stipe width narrow, with low thecal inclination.

NAME. Ξίφος, 'a sword', referring to the virgellar spine occurring in all species.

SPECIES INCLUDED. *Didymograptus formosus formosus* Bulman 1936a, *D. formosus svalbardensis* Archer & Fortey 1974 (= *D. delicatus* Braithwaite 1976), *D. elongatus* Harris & Thomas 1940, and *D. 'nitidus'*, *sensu* Braithwaite 1976; ?*D. patulus*, *sensu* Törnquist 1901 (*non* Hall 1865) (= *D. patulentis* Chen in Mu *et al.* 1979), ?*D. cypselo* Archer & Fortey 1974.

DISCUSSION. The genus *Xiphograptus* is proposed for a number of species which would have formerly been regarded as extensiform *Didymograptus*. The structure of the proximal end shows that these species are more closely related to true *Phyllograptus* (but not to *Pseudophyllograptus*) as re-evaluated in this paper than to any of the *Didymograptus* (*Expansograptus*) group. We regard the extensiform rhabdosome habit as having been independently derived. The alternative is that the proximal end structure of *Phyllograptus* and *Xiphograptus* was independently arrived at, which seems most unlikely.

It requires reasonably well preserved material to see the characteristic virgellar spine which would betray a species as belonging to *Xiphograptus* rather than *Didymograptus* (*Expansograptus*), but the spine is visible in favourably preserved flattened material. It is probable that a number of previously-described species will ultimately prove to belong to the new genus. If, during astogeny, the virgellar spine comes to lie along the ventral margin of one of the stipes it will be necessary to have growth stages to determine that the species belong in *Xiphograptus*. From the species that we can already assign with confidence to *Xiphograptus* the stratigraphic range of the genus extends through the Arenig to the Llanvirn. So far, its distribution seems to be predominantly through the Pacific Province, like *Phyllograptus*, *sensu stricto*.

? *Xiphograptus elongatus* (Harris & Thomas 1940)

Fig. 83a–c; Pl. 1, fig. 11

?1940 *Didymograptus elongatus* Harris & Thomas: 132–133; pl. 1, fig. 12A; pl. 2, figs 14A, B.

STRATIGRAPHIC RANGE. Specimens attributable to this species have been recovered from 17 m to 49 m from base, V₁b, spanning the latest Bendigonian to Chewtonian.

MATERIAL. Isolated proximal ends PMO NF3814–5; specimens on the rock include PMO NF2836 and numerous proximal ends.

DESCRIPTION. This species can be recognized both from specimens preserved in shale, and from isolated, slightly flattened examples. In most details the species closely resembles *Xiphograptus formosus svalbardensis* from the upper part of the Olenidsletta Member (Archer & Fortey 1974). The sicula is short, 1.2 to 1.3 mm long, excluding a very short nema, and the virgella, 0.7 mm long in some examples. Its aperture is 0.35 mm across, and probably broadly elliptical. The dorsal side of the sicula is prolonged into a lip and slightly curved so that the angle between the aperture and the virgella is acute. Theca 1¹ begins very high up on the sicula, probably at the base of the prosicula, and the sicula and th1¹ grow down in tandem such that 0.7 mm of the pair projects above the dorsal wall of the stipe. At about 0.3 mm from the base

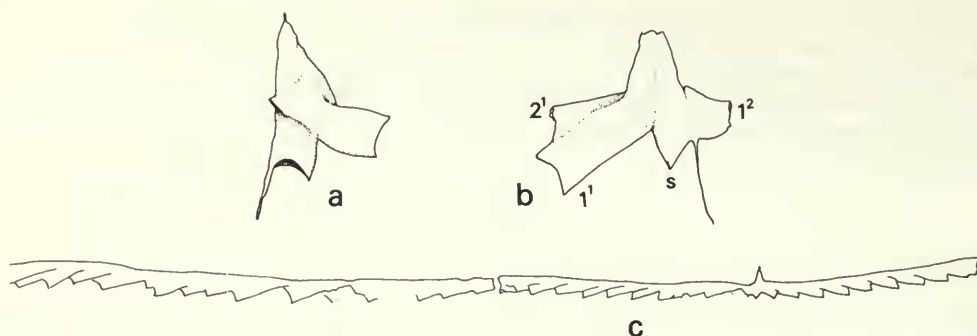


Fig. 83 ?*Xiphograptus elongatus* (Harris & Thomas), isolated, somewhat flattened growth stages and full rhabdosome. a, PMO NF3815, in reverse view showing 'hood' stage of development. b, NF3184, obverse view, showing long free ventral wall of $th1^1$. Both from 16 m above base of Olenidsletta Member on Profilstranda, $\times 18$. c, NF2836, flattened, imperfect specimen, from 17 m above base of Olenidsletta Member, Olenidsletta; $\times 3$.

of the sicula $th1^1$ takes a very sharp bend away from the sicula, such that the angle between the free wall of the sicula and the free ventral wall of $th1^1$ is 85° – 90° . The distal part of $th1^1$ beyond the bend is 0.8 mm or slightly more. At the stage of production of $th1^2$ and $th2^1$ there is a characteristic 'hood' as shown by *D. formosus svalbardensis* (Archer & Fortey 1974: fig. 4a). Development isograptid: $th1^2$ and $th2^1$ subsequently grow out horizontally, and a horizontal to slightly reclined habit appears to characterize all the specimens from Spitsbergen. Dorso-ventral stipe width at the level of the first thecae is 0.7 mm, and the maximum stipe width we have observed is 1.4 mm, with the increase being gradual in the manner of *D. extensus* (but with even lower gradient of increase). There is every reason to suppose that the stipes continued to grow and expand in width to the 2 mm mentioned as a maximum by Harris & Thomas. Thecal inclination remains low, about 20° even distally, and this is what accounts for the exceptionally low thecal spacing, 8 or 9 per 10 mm distally. Apertures were probably minutely denticulate, and the apertural margins are at an approximate right angle to the free ventral thecal walls (may appear slightly acute or slightly obtuse).

DISCUSSION. Harris & Thomas (1940) gave a somewhat perfunctory description of '*Didymograptus elongatus*' from the Bendigonian of Australia. Nonetheless their figure (1940: pl. 2, fig. 14B) clearly shows the virgella, and the long free ventral wall of $th1^1$; the very narrow stipes, their slow expansion, consistently low thecal inclination and wide distal thecal spacing are all similar on our material and that of the Australian form. But we retain a caution in our determination. The similarity to the younger species *Xiphograptus formosus svalbardensis* (Archer & Fortey 1974) is obvious. Proximal ends are distinguished by several small details: the outward bend on $th1^1$ is sharper on *X. elongatus*, so that the angle between the free part of the sicula and that of $th1^1$ is generally larger, and the length of the free ventral wall of $th1^1$ is longer on the older species. Large populations of isolated specimens of *X. formosus svalbardensis* show a variation in this length between 0.4 and 0.6 mm, with the majority of specimens 0.5 mm, whereas we have 0.8 to 0.9 mm for this measurement on *X. elongatus*. Thecal inclination is probably even lower on *X. elongatus*, which accounts for its extremely loose thecal spacing distally, fewer thecae per 10 mm than *X. formosus svalbardensis*. Our populations of *X. elongatus* include only specimens with horizontal to slightly reclined stipes, whereas *X. formosus svalbardensis* includes a proportion of declined forms. However, with very thin stipes such differences should be viewed with caution in flattened material. *X. formosus formosus* (Bulman 1936a, Skevington 1965) has consistently more strongly declined stipes, and the virgella becomes virtually incorporated in the exterior wall of $th1^2$. It is possible that there is continuous intergradation between *X. elongatus*, *X. formosus svalbardensis* and *X. formosus formosus* through the Arenig.

Harris & Thomas (1940: 132) remark that the sicula in their specimens was 'apparently slightly inclined from normal to the axis of the stipes'. This appearance is common in flattened material, and is probably produced by a combination of the distal curvature of the sicula, with the antivirgellar origin of $th1^1$ and the broad crossing canal developed from the 'hood' leading to $th2^1$.

Xiphograptus formosus svalbardensis (Archer & Fortey 1974)

Pl. 1, figs 6–8

1974 *Didymograptus formosus svalbardensis* Archer & Fortey: 91–95, text-figs 3c–g, 4a–f.

1976 *Didymograptus extensus* (Hall), s.s.; Braithwaite: 48–49: pl. 9, figs 10, 11, 13.

STRATIGRAPHIC RANGE. Upper part of Olenidsletta Member, 116–130 m above base, V_3a –b, later Arenig (Castlemainian Ca_3 = lower part of *Isograptus* Zone).

ADDITIONAL MATERIAL. In addition to the original type material PMO NF3340–1 and NF3218 are figured here.

DISCUSSION. Archer & Fortey (1974) gave a full description of this species. Here we figure proximal ends to give a more detailed illustration of proximal structure for comparison with *X. elongatus*. There is a little more variation in this species than was allowed in the original description. Whole specimens may be horizontal, gently declined or reclined. Proximal stipe width at $th1^1$ may be as narrow as 0.55 mm (0.65 mm is usual) and distal stipe fragments may be as wide as 1.3 mm. One particularly interesting specimen (Pl. 1, fig 8) show distinctive prothecal folds, an extreme development of the small undulations which are often present on the dorsal wall of isolated specimens. But in other features this specimen is typical of *D. formosus svalbardensis* and there seems to be no reason why it should be regarded as a separate species. If it is not, it follows that the presence of prothecal folds ought not to be considered a fundamental character, and such folds may be capable of polyphyletic derivation.

Distinctions from *X. elongatus* are listed above. Braithwaite (1976) described *Didymograptus delicatus* from the early Ordovician of Utah; his illustrations of the proximal end (1976: pl. 16, fig. 6) demonstrate that this is a *Xiphograptus* species. Note that the virgellate sicula figured on Braithwaite's (1976) pl. 16, fig. 2 is also likely to belong to *Xiphograptus* rather than to *Didymograptus bifidus*. Variation in rhabdosome habit and thecal proportions are much like those of our species, but some specimens are stated to be much narrower at the proximal end (down to 0.32 mm), and at the population level this may indicate a specific distinction. Braithwaite gives the locality as from the Kanosh Shale: Archer & Fortey figured some Utah specimens from stratigraphically below this (shales beneath the Juab Limestone) which are undoubtedly conspecific with the Spitsbergen species, and of about the same age. This is probably what Braithwaite recorded as *D. extensus* (Hall). So *X. formosus svalbardensis* does occur in Utah, and may there extend into younger beds or be represented therein by closely related species. Braithwaite's *D. 'nitidus'* is another *Xiphograptus* altogether more robust than *X. formosus* subsp.

X. formosus svalbardensis is an extremely abundant species in the Spitsbergen Ordovician, and it would be surprising if it were not geographically widespread. It seems possible that some of the records of *D. extensus* from the younger Arenig may refer to this form. Some slender late Arenig didymograptids have been described with proportions not unlike those of the Spitsbergen species. For example *D. slemmestadi* Monsen 1937 appears to be generally similar, apart from slightly closer distal thecal spacing; Monsen indicates a normal dichograptid proximal end for this species (1937: pl. 2, fig. 10; also Mu *et al.* 1979: pl. 35, figs 22–24), and if this is correct it cannot be conspecific with the Spitsbergen form. A slender species of '*Didymograptus*' from the Arenig of New Zealand (Cooper 1979: pl. 12, fig. a) may also prove to be referable to this species.

Xiphograptus patulentis (Chen in Mu *et al.* 1979)

Pl. 1, figs 9, 10

1901 *Didymograptus patulus* (Hall); Törnquist: 15–17; pl. 2, figs 1–6.1979 *Didymograptus patulentis* Chen in Mu *et al.*: 105–106; pl. 36, figs 5, 20, 21; pl. 37, fig. 1.

STRATIGRAPHIC RANGE. Upper part of Olenidsletta Member, 122 m from base, V₃b (upper Arenig, Castlemainian Ca₃).

MATERIAL. SM A105821–3.

DESCRIPTION. Only one specimen preserves a good proximal end. Stipes diverge at 180°, to become slightly reclined distally. Sicular about 1.8 mm long, with prominent virgella proving the assignment of this species to *Xiphograptus*. Stipe width at th1¹ is 1 mm, and the increase in stipe width is rapid, such that at the fourth or fifth theca it is 2 mm or more. Isolated stipes from the same bedding plane attain a width of 3 mm, a width that remains virtually constant over stipe lengths exceeding 3 cm. There seems to have been some variation in distal stipe width, but with proximal expansion rapid, much in the manner of *D. patulus*. Distal thecal spacing is exactly 10 thecae in 10 mm on available material. The 'cut away' appearance of the thecal apertures is characteristic, such that the free ventral thecal wall makes an angle of about 45° with the apertural profile. Thecal inclination distally 40°–50°.

DISCUSSION. Chen (in Mu *et al.* 1979) renamed the species described by Törnquist (1901) as *Didymograptus patulus* (Hall), noting that Törnquist's specimens differed in several respects from Hall's type material. We use the name *patulentis* Chen here, because our material compares closely with Törnquist's specimens, which are from the higher Arenig of Sweden (*D. patulus* is probably from the earlier Arenig). Törnquist's original description states 'In one specimen I have seen a filiform appendice projecting from the corner of the (sicular) aperture in every respect resembling the virgella . . .' This is a clear indication that Törnquist's specimens belong to *Xiphograptus*; Törnquist's (1901) pl. 2, fig. 4 shows isograptid development. Since *D. patulus* is apparently a normal *Didymograptus* (*Expansograptus*) it cannot be conspecific with the younger species from Sweden, nor with our material from Spitsbergen. Although Törnquist mentions a sicular as long as 3 mm his figures indicate a length of 2 mm or less, not greatly different from our material. Of specimens attributed to *D. patulentis* from south-west China only one (Mu *et al.* 1979: pl. 37, fig. 1) shows what is probably the virgella on the left of the sicular. There too the species occurs in high Arenig strata. The general growth of the stipes and the thecal form are very like *Didymograptus patulus*, but this must be a matter of parallel evolution. There has been the suggestion (e.g. Spjeldnaes 1953: 178) that *D. patulus* gave rise to *D. hirundo*. Spjeldnaes appears to refer to Törnquist's material in his account; since *hirundo* is as far as we can tell a normal *Didymograptus* (*Expansograptus*), *Xiphograptus patulentis* is not likely to be its ancestor.

Xiphograptus ? cypselo (Archer & Fortey 1974)1974 *Didymograptus cypselo* Archer & Fortey: 89–91, text-figs 1, 3a, b.

STRATIGRAPHIC RANGE. Upper part of Olenidsletta Member, 116–130 m above base, V₃a, associated with *Pseudotrigrionograptus minor* (late Arenig Ca₃).

REMARKS. There is nothing to add here to the description of Archer & Fortey (1974) except to note that the isolated proximal end (1974: 90) suggests that this species should now also be referred to *Xiphograptus*. The interpretation of that specimen may have been in error, with th1¹ lying on the antivirgellar side in the usual way for *Xiphograptus*. Since all the available specimens of *X. cypselo* have been secondarily greatly thickened interpretation of thecal order is difficult. The holotype is a specimen preserved on the rock, and because the virgellar spine has not been noted on that specimen, the attribution to *Xiphograptus* is tentative pending the recovery of more isolated material. The resorption of the sicular appears to be characteristic of *X. ? cypselo*, but may be difficult to recognize in flattened material, and as with *X. formosus svalbardensis* there is the possibility of unrecognized synonyms in the literature.

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